

CHICKASAW PLUM: ESTABLISHMENT AND
IMPORTANCE OF INTEGRATION AMONG RAMETS

By

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CHICKASAW PLUM: ESTABLISHMENT AND
IMPORTANCE OF INTEGRATION AMONG RAMETS

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CHAPTER I

Introduction

For many wildlife species, shrubs are often the only substantial cover from predators and thermal stress available in arid and semi-arid systems. The clonal nature of many shrubs aids survival in the relatively harsh environments they occupy and is a useful characteristic for creating woody canopy cover. Chickasaw plum (*Prunus angustifolia* Marsh.) is a commonly occurring shrub which has a native range covering the southern Great Plains and the southeastern quarter of the United States. This plant is gaining attention as a vital element for wildlife in the southern Great Plains where Northern Bobwhite (*Colinus virginianus*) habitat is often limited by the amount of woody cover. Many other wildlife species rely on woody patches in grasslands for various reasons such as nesting, hunting, or food sources. In addition to Chickasaw plum, smooth sumac (*Rhus glabra* L.) and fragrant sumac (*R. aromatica* Aiton) are common species with widespread native distributions that, once established, will spread clonally. This growth habit may allow for the establishment of cover to provide habitat for wildlife species. Additionally, understanding the physiological processes driving the growth and expansion of Chickasaw plum will allow land managers to make informed decisions about habitat manipulation in grassland ecosystems.

Two experiments were conducted in 2007 and 2008. In the first study, small stands of the plum and two sumac species were established to determine effective practices to establish small stands of native clonal shrubs for improving wildlife habitat in northwestern Oklahoma and similar regions. The specific objectives were to determine effects on survival and growth of 1) propagule source, i.e., nursery-grown bare-root seedlings, intact local transplants, and coppiced local transplants, 2) tillage and interspecific competition control, and 3) planting date.

In the second study, the roots of interconnected ramets within existing stands of Chickasaw plum were severed to gain insight on the process of resource integration by determining the relative importance of persistent root connections between ramets. To achieve this carbon gain (photosynthesis and growth) and water relations (stomatal conductance, intercellular CO₂, stem midday water potential, and soil volumetric water content) were monitored for differences between stems that had their root connections severed or those that did not.

CHAPTER II

Review of Literature

CLONAL PLANTS

Vascular plants share many general life strategies that include the maximization of seed-bearing lifespan, the genesis of transport tissues that distribute resources and provide structural support to the plant as well as traits that promote successful competition for resources above and belowground (Jenik 1994). Reproduction is accomplished through two mechanisms; sexual and asexual. Sexual reproduction results in a new individual plant via a seed that is generated as a result of pollination. Plants that propagate asexually generate new potentially independent plants that are the result of vegetative growth (Jenik 1994; Alpert 1999; Stenvall et al. 2004; Vaughan et al. 2007; Beaudet and Messier 2008). These plants contain identical genetic material and are known as clones. Clonal growth is defined by an organism's ability to produce multiple repetitions of developmental units that have the potential to be physiologically autonomous (Oborny and Kun 2001). An entire clone is known as a genet and each potentially functionally independent module is known as a ramet (Eriksson 1993).

Clonal growth facilitates a competitive advantage by increasing the lifespan of a genet and successfully gathering and allocating resources. Clonality is a strategy that plants employ that increases their ability to produce successful offspring (Bond and Midgley 2003). Many clonal plants appear to use a sit-and-wait strategy in which they expand for many years and periodically disperse high numbers of seeds. This creates a higher probability of success when germination conditions are ideal (Hosaka et al. 2005).

Clonal growth can be exhibited several ways and is achieved by sprouting from dormant, suppressed, or adventitious buds (Esau 1977; Bosela and Ewers 1997). Specialized organs usually are in the form of modified stems including rhizomes, bulbs, corms, stolons, and tubers. Most research conducted on clonal mechanisms has been performed on herbaceous plants. These processes are fairly well understood across a wide spectrum of non-woody plants (Alpert 1996; Derner and Briske 1998; Yu et al. 2002). However, relatively less is known about the ecology and physiology of clonality in woody perennials. The mechanisms driving sprouting in woody plants originate from dormant endogenous or adventitious buds in the roots, at the base of stems that have been damaged, from the root collar, or from branches that are contacting the ground. The roots of woody plants can act as carbohydrate storage organs that bear meristems that generate new roots and stems. This suckering system is demonstrated by several woody species (DeByle 1964; Petranka and McPherson 1979; Jenik 1994).

It is difficult to distinguish between the mechanisms driving sprouting of new ramets whether it be spontaneous, damage induced, hormonal, some other driver, or a combination of these (Luken 1990; Hosaka et al. 2005). Jenik (1994) divided clonal growth of woody plants into three categories: 1) repeated copies of reproductive modules

by primary meristems in the form of additional buds, 2) reiteration of damaged and aging organs, and 3) initiation of new organs from adventitious (or reparative) buds. Clonal plants will produce additional stems as part of their natural growth progression (Del Tredici 2001). In plants that sprout during normal growth, apical dominance is not the controlling process. These sprouts arise from dormant buds that are formed endogenously in young undamaged roots, at the root collar, or from stems that have been buried (Del Tredici 2001; Lantz and Antos 2002; Dunkin et al. 2008). These buds remain attached to the primary xylem by trace elements as the diameter of the root increases (Fontaine et al. 1999). They will branch to form bud clusters, but fail to remain active indefinitely and very mature roots and stems lose their ability to sprout (Smith et al. 1997).

Disturbances will elicit a sprouting response in a vast number of plants (Landhausser and Lieffers 2002; Bond and Midgley 2003; Hosaka et al. 2005). A disturbance to aboveground stems that causes a loss in leaf area will increase the root-to-shoot ratio which will initiate a sprouting event by sending hormonal cues to inactive buds that releases them from apical dominance (Landhausser and Lieffers 2002; Fraser et al. 2004; Beaudet and Messier 2008). Reparative buds form near the surface of the root so they are disjunct from the pith and are activated less frequently (Esau 1977; Bosela and Ewers 1997). The newly sprouted buds draw on the carbohydrate reserves in the remaining stems and roots and the vigor of sprouts is positively correlated to levels of carbohydrate in storage (Willard and McKell 1978; Cerasoli et al. 2004).

There are many advantages to having a clonal growth form including rapid establishment, the ability to integrate resources among connected ramets, and a

potentially unlimited lifespan. Clonal plants have the ability to buffer the effects of resource heterogeneity on a small scale; i.e. the area occupied by interconnected clones (Herben 2004). This trait may (Wijesinghe and Handel 1994) or may not (Peltzer 2002) increase the competitive ability of the plant. It has been demonstrated that root suckers of beech (*Fagus grandifolia* Ehrh.) have greater height, diameter, and survivorship than seedlings. This jumpstart on growth provides an increase in the plant's competitive ability (Beaudet and Messier 2008). Honnay and Bossuyt (2005) note that environmental and spatio-temporal stochasticities are buffered by clonal species more than non-clonal species due to the iteration of ramets and potential for resource integration. Moreover, clonal plants are more buffered against spatio-temporal heterogeneity in the habitat due to the potential reallocation of resources among ramets. Hosaka et al. (2005) identified three main factors that contribute to clone persistence in pawpaw (*Asimina triloba* L.); 1) Ramet iteration reduces the probability of genet mortality due to stochastic disturbances, 2) Integration promotes the establishment of new ramets on less than ideal sites, 3) Horizontal expansion improves access to heterogeneously distributed resources. Clonal plants are generally more resistant to disturbance or local extinction than species that lack the ability to reproduce asexually (Honnay and Bossuyt 2005). This is largely due to their ability to buffer environmental heterogeneity in space and time (Eriksson 1993).

Sprouting controls the persistence of a clone's life after disturbance and the acquisition of new territory and resources (Del Tredici 2001). Bond and Midgley (2003) stated that a clone may occupy the same place for millennia with little change in population size. This allows for very long term if not unlimited fecundity of a clone and increases the probability that the successful genetic make-up from that clone is passed on

to future generations when seedlings are successfully established (Eriksson 1993). As a result of the long lives and lack of senescence in many clonal plants, it is often difficult to identify a genet without the aid of genetic tests. However, in some species like aspen (*Populus tremuloides* Michx.) and Chickasaw plum, a clone may be identified by phenotypic traits like leaf color in fall or timing of flowering in spring, respectively (D. Bartos, personal communication, August 2008). Plum clones form a stand with hill structure and are generally distinct from other clones. Aspen populations are more genetically inter-mixed as a result of mass germination events that occur in response to disturbance such as after major fires (Turner et al. 2003). The above examples illustrate the two major clonal growth strategies that exist on a spectrum spanning from integrators which possess connections that persist for long periods of time like Chickasaw plum to splitters whose connections are short lived like aspen (Oborny and Kun 2001).

Splitter describes the habit of a genet to spread across the landscape as separate and independent ramets. Connections between ramets are short-lived. Once the new ramet is functionally independent, it need not rely on resource subsidies from its mother plant. This allows a species to spread out on a landscape in search of patches of good resource availability. A good site will allow the ramet to thrive and reproduce sexually and/or initiate new ramets. This habit allows the plant to most thoroughly use the available resources.

Integrator plants possess persistent connections between the ramets. This strategy allows for each stem to acquire nutrients, carbon, and water and subsequently translocate them to nearby ramets in less rich patches. This method of gathering resources allows for the genet to occupy a site with patchy resources, but the ramets on resource poor sites can

persist because they are subsidized by the rest of the genet with limiting resources (Evans 1988). This allows for all ramets to remain a viable source of seed regardless of site quality as long as some ramets can provide the necessary resources for its own growth and have a surplus to sustain efficient ramets.

Ramet population sizes tend to stabilize depending on species and environment. The mechanism controlling this population density has been suggested to be due to limits of integration or a modular control of bud initiation (Eriksson 1993). The extent of the area occupied by any single clone is dependent on the species but splitters have a greater potential to spread which is exemplified by the Pando clone in Utah that may be the largest living organism on the planet (Mitton and Grant 1996).

SHRUB ECOLOGY

Shrubs are woody plants that are generally short in stature and will produce multiple stems as a normal part of their development (Del Tredici 2001). Shrubs are often found on sites that are inhospitable for many trees due to climatic stress or disturbance regimes. Their clonal structures allow them to access heterogeneously distributed resources (light, nutrients, and soil moisture) in harsh environments (Schenk 1999; Yu et al. 2002; Roiloa and Retuerto 2006). In addition to normal expansion, sprouting allows for resilience to disturbances such as fire, flood, defoliation, or mechanical damage (Brommit et al. 2004; Gibson et al. 2004; Rood et al. 2007; Beaudet and Messier 2008).

Shrubs play an important role in rangelands, deserts, and forest understories. Shrubs can facilitate succession at a site by displacing shade intolerant herbaceous species and providing an environment that allows the establishment of more shade tolerant tree species. Many organs of winged sumac (*Rhus copallina* L.) including flowers, leaves, fruits, and rhizomes contain allelopathic toxins that have been demonstrated to inhibit the growth or germination of many prairie plants (Petranka and McPherson 1979). Shrubs may improve soil fertility with nitrogen rich litter and facilitate their own invasion into grasslands because many prairie species cannot take advantage of higher nitrogen levels associated with decomposition of higher N in litter (McCarron and Knapp 2001; Siemann and Rogers 2003).

Shrubs provide thermal cover for many animals and afford protection from predators. Northern Bobwhite (*Colinus virginianus*) habitat is limited by the amount of woody cover on a site (Guthery et al. 2005). Many other wildlife species rely on woody patches in grasslands. The seeds of shrubs are often larger than the seeds of forbs and grasses and may be an important source of food for many species including insects, mammals, and birds (Meyer and Pendleton 2005). White-tailed deer (*Odocoileus virginianus*) rely on shrubs for screening cover and browse. Dunkin *et al.* (2008) found nine bird species in Oklahoma nesting in mature stands of Chickasaw plum including Bell's vireo (*Vireo bellii*) and painted bunting (*Passerina ciris*), two species of concern. Insectivores find many kinds of larvae concentrated on shrubs and pollinators find an abundance of nectar on the numerous flowers produced by some species of shrubs.

Chickasaw plum, smooth sumac (*R. glabra* L.), and fragrant sumac (*R. aromatica* Aiton) are common species native to northwestern Oklahoma that, once established, will

spread clonally via root suckers. This growth habit may allow for the establishment of ample cover to provide the habitat needs for wildlife species. Additionally, planting these species on abandoned agriculture fields will help with the restoration of native habitats.

CHICKASAW PLUM

Chickasaw plum is a clonal shrub with a wide range that extends from the Southern Great Plains east to New Jersey and south to Florida. It tolerates a wide range of climatic variables and soil types, but seems to occur mostly in well drained and sandy soils (Gilman and Watson 1994). A single stem can grow to about 3 m. Plum will establish by seed and after 2 years will begin to initiate new ramets from its roots. Dunkin et al. (2008) found that plum clones in Oklahoma expand at a rate of $31 \text{ m}^2 \text{ y}^{-1}$ and can cover an area $>1 \text{ ha}$. The oldest stem in their survey of 95 clones was 27 years. Clones have distinct growth pattern. If stands are undisturbed, the mother plant will be the tallest individual with the widest diameter near the middle of the thicket and new ramets will initiate at the periphery in subsequent years. The term “motte” (from French: hill) is used in the southern United States to describe this growth habit. Chickasaw plum is common in grasslands and can often be found at forest edges.

More than 40 species of birds use or are associated with plum in Oklahoma (Dunkin et al. 2008). Several other taxa including mammals, reptiles, and insects use plum in various capacities. Plum provides cover from predators and relief from thermal

stress. In a good year plums will produce large quantities of mast that is used by but not relied upon by numerous animals (deer [*Odocoileus virginianus*], raccoons [*Procyon lotor*], coyotes [*Canis latrans*], and insects). McCarty *et al.* (2002) found that about 85% of the fruits of Chickasaw plum are eaten by wildlife 3 days after ripening.

Chickasaw plum has broad cultural significance. Cattlemen dislike plum because it will occupy the space that would otherwise have grass that cattle could graze. There has been a history of shrub control efforts in rangelands. Native Americans widely used plum for food (Carlson and Jones 1940). Chickasaw plum is popular for making wines and jellies (Gilman and Watson 1994).

SMOOTH SUMAC

Smooth Sumac is a widely distributed shrub whose range includes the entirety of the North American continent except Alaska and the Arctic provinces of Canada. It is a pioneer species that tolerates a wide variety of site conditions but seems to prefer poor or disturbed soils in prairies, rocky hillsides or woodland openings (Hurteau 2004). Stems can grow to 3 m and clones reiterate and spread via root sprouts. A clone will spread laterally at a rate of 1 m y^{-1} (Gilbert 1966). It has been demonstrated in *R. glabra* and conspecifics that sprouting rates may be increased by a disturbance such as fire or heavy browsing (Knapp 1986; Strauss 1991). *R. glabra* clones exhibit a motte structure similar to that of plum. This species may be propagated by seed or root cuttings (Hurteau 2004). The seeds of many *Rhus* species are used throughout the winter by a number of birds,

mammals, and insects (Jewell et al. 1991; Strauss 1991; McCarty et al. 2002). There is a long history of smooth sumac being used by Native Americans for medicines, food, and dyes (Hamel and Chiltoskey 1975).

FRAGRANT SUMAC

Fragrant sumac occupies the eastern half of North America from the Atlantic Ocean to the Great Plains (Taylor 2004). Plants can reach 1.5 m. Thickets are formed when the branches contact the ground and adventitious roots become established in a process known as layering. This species thrives in dry forests or rangelands. *R. aromatica* is also an abundant producer of seed that can be used as a winter food source for many taxa (Nantel and Gagnon 1999). It is a pioneer species and the seeds will germinate readily after a heavy disturbance. *R. aromatica* will sprout vigorously from the root crown following a defoliating disturbance event such as fire. Ramets may live 20 – 30 years. Propagation is achieved by growing seedlings or taking root cuttings. Fragrant sumac has ethnobotanical uses that include food, medicine, and tanning (Reagan 1928).

SHRUB ESTABLISHMENT

Establishing native shrubs on prairie or fallow farmland is achieved two ways, direct seeding or planting seedlings. Seeding an area has the advantage of potentially

establishing large areas for relatively low cost and labor. Seeds of shrubs can be included in seed mixes for native plant restoration and applied to restore native diversity, regenerate food sources, and mitigate wind and water erosion from degraded lands (Grantz et al. 1998; Visser and Botha 2005). However, success rates are low because seed mortality is very high and competition from existing plants limits seedling establishment. Additionally, it may be difficult to obtain large quantities of native seed. An alternative to direct seeding is nursery produced seedlings. These have the advantage of high survival rates, but seedlings must be planted by hand and the labor involved restricts the scope of the planting area (Johnson and Okula 2006). Furthermore, seedlings have a one or two growing season head start compared to seeds. The positive results obtained using seedlings make the increase in cost and labor requirements often worth the investment depending on the required planting density.

Use of seedlings in forestry and conservation plantings is well established, occurring on approximately 1 million hectares annually (Smith and Darr 2002). Over 1 billion seedlings (96% bare-root) were planted during the 2005 – 2006 season in the Southern United States with 1.7 million of those in Oklahoma (McNabb and Eneback 2009). Many states have a nursery that produces seedlings to support these efforts. For instance, the state seedling nursery in Goldsby, Oklahoma, sells bare-root hardwood seedlings of >30 species for \$0.05 – \$0.60 (depending on species and quantity purchased). Containerized seedlings, which contain an intact root-soil interface, are available for marginal sites for approximately \$0.90 each.

Often the most limiting factor for seedlings establishment in the first year after transplanting is water stress because root systems are initially poorly developed.

Coppicing is a cultural treatment that entails severing the aboveground portion of a plant and is used to alter the root-to-shoot ratio. In most angiosperms this produces a sprouting response that uses stored energy in the roots to produce new, vigorous stems (Smith et al. 1997). Removing the existing buds from a transplanted stem reduces water stress on the plant because of the resulting increase in the root-to-shoot ratio and may increase establishment success. This method is used in forestry for short rotation crops like aspen (Shepperd 1996) or to prevent the need for replanting like in chestnut (*Castanea sativa* Mill.) (Giudici and Zingg 2005).

Transplants, i.e., seedlings or ramets that are dug up and replanted elsewhere, may be taken from local sources if seedlings are not commercially available, the cost of seedlings is prohibitive, or a particular genet is desired. Local transplants have genetics that are well adapted to its site and could provide a viable option for stand establishment. Often, the ability of a cutting or transplant to establish a viable clone is positively correlated with the amount of mobile carbohydrate reserves and its size or biomass (Ghani and Cahalan 1991; Ritchie et al. 1993; Landhausser and Lieffers 2002). More sophisticated propagation techniques involve the micropropagation of small groups of cells in undifferentiated somatic tissue in the seeds or meristems (Merkle et al. 1997; Dean 2008). All of these methods result in independent plants that may be planted in the field.

Tilling is a common method for site preparation (Karlsson 2002; Blazier and Dunn 2008). It has agricultural as well as natural resource management applications (Ducci and Santi 1997; Johnson and Okula 2006). Tilling physically disturbs the soil, reduces competing vegetation, exposes a site to more sunlight, and improves water

infiltration and root penetration (Lincoln et al. 2007). Carlson *et al.* (2006) found that tillage had a positive effect on survival of loblolly pine (*Pinus taeda* L.) seedlings on some Piedmont sites across the southeastern United States. Tillage improved height and diameter growth of loblolly pine seedlings on the Upper Coastal Plain and Piedmont of Georgia on a wide range of soil types (Wheeler et al. 2002; Lincoln et al. 2007). Karlsson (2002) showed that silver birch (*Betula pendula* Roth) seedlings had increased survival on sandy soils with deep plowing. On upland sites, tillage increases growth primarily by increasing the penetration ability of roots (Will et al. 2002). In degraded rangelands, tillage has been shown to increase species diversity and plant density (Huffman 1997; Van der Merwe and Kellner 1999; Visser and Botha 2005).

Plants in close proximity will compete for soil water and mineral resources and light (Fuhlendorf et al. 1997; Herben 2004; Tworkoski and Glenn 2001). Competition control increases growth by allowing desired plants to utilize site resources more completely (Smith et al. 1997). Chemical herbicides, physical barriers, or mechanical treatments can be used to achieve this goal. The herbicide sulfometuron methyl increased survival and growth of cottonwood (*Populus deltoides* Bartram ex Marsh.) seedlings compared to cultivation and physical barriers (Geyer et al. 2006). Sulfometuron methyl applied over longleaf pine (*P. palustris* Mill.) seedlings increased diameter growth and the rate at which seedlings emerged from the grass stage (Ramsey and Jose 2004). In another study, sulfometuron methyl reduced hardwood regeneration growth except in combination with lime to increase soil pH (Schreffler and Sharpe 2003).

Alternative to herbicide, weed barrier fabric can also increase the survival and/or growth of seedlings by depriving unwanted weeds of light (Davies 1988). Weed barrier

cloth increased survival of cottonwood compared to other synthetic mulches (Geyer et al. 2006) and increased height growth for newly established Arizona cypress (*Cupressus arizonica* Greene) seedlings compared to no treatment in New Mexico (Harrington et al. 2005). Mechanical treatments to reduce interspecific competition include mowing, cultivating, or hand weeding periodically around the desired species (Snyder 1982; Huffman 1997; Woeste et al. 2005).

DETECTING THE MOVEMENT AND ALLOCATION OF RESOURCES

Clonal plants have the potential to share resources, e.g., water, nutrients, and carbohydrates, between connected ramets (Evans 1988; deKroon et al. 1996; Herben 2004; Roiloa and Retuerto 2006). Measuring movement of resources in clonal plants has been accomplished in several different ways. Most research has focused on herbaceous plants because of the ease with which controlled experiments can be conducted (Alpert 1999; Eriksson 1993; Herben 2004; Zhang et al. 2008). Woody clonal plants pose problems for experimenters due to slow growth rates and large clone size. Generally studies on woody plants are conducted *in situ* and it is often difficult to eliminate confounding factors (Eriksson 1993). Evaluating the mechanisms of short-term physiological processes on clonal growth and survival of long-lived woody plants can be a challenge. The most basic way to observe connections is to physically excavate the roots. Excavating root samples for analysis of larger plants proves to be a difficult task (Eriksson 1993; Jenik 1994; Mayes et al. 1998). Boo and Pettit (1975) explored the root

structure and carbohydrate reserves in shinnery oak (*Quercus havardii* Rydb.) by removing the A-horizon of the soil profile with a fire hose, but this method is not common. They found that mechanical disturbance caused root carbon reserves to decrease during early summer. This implies that carbohydrate reserves are transported to new or existing stems to aid in repair and renewal. Dyes and deuterium have been used as tracers in xylem to detect the presence, pathways, and mechanisms of the functional connections between ramets of aspen (DeByle 1964), *Carex* spp. (deKroon et al. 1996), and the shrub *Hedysarum leave* (Zhang et al. 2003). Labeling using the carbon isotopes ^{13}C and ^{14}C has been used to track the movement of photosynthate through clonal fragments and forest stands (Dyckmans and Flessa 2001; Keel et al. 2006). Zhang et al. (2002) used a ^{14}C label to track C allocation and showed that in *H. leave* daughter ramets are a much greater sink than mothers and that rhizomes are storing newly assimilated C from both stems. Additionally, defoliation induced C subsidy from the ramet left undisturbed. Plants also can be wounded (either roots or stems) to observe resource allocation among ramets after disturbance. The movement of carbon is inferred from the growth rate and location or density of new sprouts (Boo and Pettit 1975; Matlack 1997; Fraser et al. 2004; Gibson et al. 2004; Giudici and Zingg 2005).

Fertilizer was applied to largeleaf pennywort (*Hydrocotyle bonarienses* Comm. ex Lam.) clones and N integration among ramets and increased branching was observed illustrating this species' ability to exploit patchy resources across the landscape (Evans 1988). Targeted ^{15}N enriched fertilizer applications have been used to track nutrient uptake and integration in rhizomatous perennials (Evans 1988; Derner and Briske 1998; BassiriRad et al. 1999; Millard et al. 2006). It must be noted that using isotope labels is

expensive and if radioactive isotopes are used special precautions must be taken.

Monitoring changes in growth can be achieved by taking stem density data, recruitment surveys, or genetic analysis at the stand scale or heights, diameters, and biomass for individual stems (Doust and Doust 1988; Cirne and Scarano 2001; Feng et al. 2004; Nagamitsu et al. 2004; Hosaka et al. 2005). Plants have been subjected to wounding (either roots or stems) to observe resource allocation after disturbance. The movement of carbon is inferred from the vigor and location of sprouts (Boo and Pettit 1975; Matlack 1997; Fraser et al. 2004; Gibson et al. 2004). A common method for creating disturbance on a site that will encourage sprouting is coppicing. This is done by cutting stems to the ground which stimulates the emergence of new stems (Giudici and Zingg 2005).

Many clonal plant species rely on resource integration to support adjacent new ramets or transfer resources from ramets in resource-rich patches to ramets in resource-poor patches (Wijesinghe and Handel 1994; Railing and McCarthy 2000; Zhang et al. 2003; Herben 2004). There is also evidence that resource integration is not vital to all clonal species (Pauliukonis and Gough 2004; Wang et al. 2004; Poor et al. 2005; Matlaga and Sternberg 2009). When resource sharing occurs, growth of ramets providing the resource subsidy may not be affected due to increases in resource use efficiency (Zhang and He 2009) which may mask the importance of resource sharing. Resource subsidies may be most apparent on sites where resource availability is particularly heterogeneous or abundant (Alpert 1999; Herben 2004; Zhang et al. 2008). Alternatively, rather than resource integration, the function of persistent connections in the grass *Psammochloa villosa* Trin. has been shown to be an effective adaptation to withstand wind erosion in dry climates (Yu et al. 2008).

CHAPTER III

Shrub Establishment in Northwestern Oklahoma

ABSTRACT

Shrubs play an important role for wildlife in grasslands by providing cover and food. I tested the effects of tillage, planting date, and competition control on the survival and growth of different propagule types (bare-root seedlings (BRS), coppiced transplants (CT), and intact transplants (IT)) of Chickasaw plum (*Prunus angustifolia* Marsh.), smooth sumac (*Rhus glabra* L.), and fragrant sumac (*R. aromatica* Aiton). Tillage did not affect survival or growth. After 2 years, plum BRS had >50% higher survival than CT and IT. Planting in late spring increased survival of plum CT by >33%. Competition control with weed barrier cloth increased plum survival by 13% and growth by 0.5 mm in the first year. For smooth sumac, there were no differences in survival and growth between CT and IT and survival was 49% after 2 years. For fragrant sumac, 83% of BRS survived after 2 years. Overall, BRS performed well, but if seedlings are not available, local transplants can be taken and planted at higher densities to achieve similar results.

Keywords

bare-root seedling, coppice, *Prunus angustifolia*, *Rhus aromatica*, *Rhus glabra*, transplant

INTRODUCTION

Chickasaw plum (*Prunus angustifolia* Marsh.) is a commonly occurring shrub which has a native range covering the southern Great Plains and the southeast quarter of the United States (Little 1977). This plant is gaining attention as a vital element for wildlife in the southern Great Plains (Dunkin et al. 2008) where Northern Bobwhite (*Colinus virginianus*) habitat may be limited by the amount of woody cover. Shrubs provide thermal cover as well as protection from predators. Bobwhites show a preference for habitats with mixed shrub cover compared to habitats lacking shrubs for coverts in summer and roosts in winter (Guthery et al. 2005). Many other wildlife species rely on woody patches in grasslands for various reasons such as nesting, hunting, or food sources (Jewell et al. 1991; Gee 1994). In addition to Chickasaw plum, smooth sumac (*Rhus glabra* L.) and fragrant sumac (*Rhus aromatica* Aiton) are common species with widespread native distributions that, once established, spread clonally via root sprouts (Knapp 1986; Nantel and Gagnon 1999). This growth habit may allow for the rapid establishment of cover to provide the habitat needs for wildlife. Development of effective methods for native shrub establishment in grasslands is important for managers who desire to increase cover and food provided by shrubs.

Initial establishment of native shrubs on prairie or fallow farmland is achieved two ways, direct seeding or planting seedlings. Seeding an area has the advantage of potentially establishing large areas for relatively low cost and labor. Seeds of shrubs can be included in seed mixes for native plant restoration and applied to restore native diversity, regenerate food sources, and mitigate wind and water erosion from degraded lands (Grantz et al. 1998; Visser and Botha 2005). However success rates are low because seed mortality is high and competition from existing plants limits seedling establishment. Additionally, it may be difficult to obtain large quantities of native seed.

Alternatives to direct seeding are nursery produced seedlings and local transplants. Seedlings must be planted by hand and the labor involved restricts the scope of the planting area (Johnson and Okula 2006). The positive results obtained using seedlings make the increase in cost and labor requirements often worth the investment depending on the required planting density. Transplants, i.e., seedlings or ramets that are dug up and replanted elsewhere, may be taken from local sources if seedlings are not commercially available, the cost of seedlings is prohibitive, or a particular genet is desired. While transplants can be gathered free of charge, labor involved with collecting, transporting, and replanting is greater than for nursery produced seedlings.

Often the most limiting factor for seedlings establishment in the first year after transplanting is water stress because root systems are initially poorly developed. Coppicing is a cultural treatment that entails severing the aboveground portion of a plant and is used to alter the root-to-shoot ratio. In most angiosperms this produces a sprouting response that uses stored energy in the roots to produce new, vigorous stems. Removing the existing buds from a transplanted stem reduces water stress on the plant because of

the resulting increase in the root-to-shoot ratio and may increase establishment success. This method is used in forestry for short rotation crops and horticulture for plant propagation (Ghani and Cahalan 1991; Giudici and Zingg 2005).

Tillage and interspecific competition control are common methods of site preparation in forest and range systems (Blazier and Dunn 2008; Karlsson 2002; Romo and Grilz 2002). Tilling physically disturbs the soil, reduces competing vegetation, exposes a site to more sunlight, and improves water infiltration and root penetration (Lincoln et al. 2007). Herbicide use is a common practice that reduces competition to the desired species (Ramsey and Jose 2004; Schreffler and Sharpe 2003). Alternative to herbicide, weed barrier fabric increases the survival and/or growth of seedlings (Davies 1988).

My goal was to determine effective practices to establish small stands of native clonal shrubs for improving wildlife habitat in northwestern Oklahoma and similar regions. For the first year of the study the specific objectives were to 1) determine differences in survival between nursery-grown bare-root seedlings, intact local transplants, and coppiced local transplants, 2) determine the effects of tillage and interspecific competition control on the survival and growth of newly established stands of shrubs, and 3) test the suitability for stand establishment of three common shrub species (Chickasaw plum, smooth sumac, and fragrant sumac) that are important wildlife habitat in the Southern Great Plains. In the second year of the study, another site was added to test 1) whether time of planting (late winter, early spring, and mid-spring) affects survival and growth of shrubs, and 2) the effects of weed barrier cloth on propagule growth.

METHODS

Study Area

Two sites were established on private lands near Waynoka, Oklahoma (Woods County) in early spring 2007 and sampled during the 2007 and 2008 growing seasons. The establishment sites were located in native bluestem (*Schizachyrium scoparium* Michx.) prairie and abandoned agricultural fields. Soils were deep loamy fine sands in the Eda and associated series (USDA-NRCS 2008). These soils are excessively drained, thermic lamellic ustipsamments and are located on undulating dunes of alluvial plains. Site 1-2007 (N 36.58, W -98.78) consisted of an abandoned agricultural field and included common sunflower (*Helianthus annuus* L.), buffalo bur (*Solanum rostratum* Dunal), sand bur (*Cenchrus* sp. L.), and goldenrod (*Solidago* sp.) with stands of Chickasaw plum, smooth sumac, and fragrant sumac among the herbaceous vegetation. Site 2-2007 (N 36.61, W -98.79) was an abandoned agricultural field dominated by common sunflower and sand bur. An additional site (Site 3-2008, N 36.51, W -98.69) was installed in 2008 on an area containing native bluestem prairie. The primary land uses for all sites were cattle grazing and hunting. The 30-year average annual precipitation for Woods County is 68 cm (Oklahoma Climatological Society 2009). Local precipitation was measured and total rainfall in the area was 91 cm in 2007 and 60 cm in 2008 (Fig. 3.1). Temperatures ranged from -18 C in February to 42 C in June 2007. There were similar extremes in 2008.

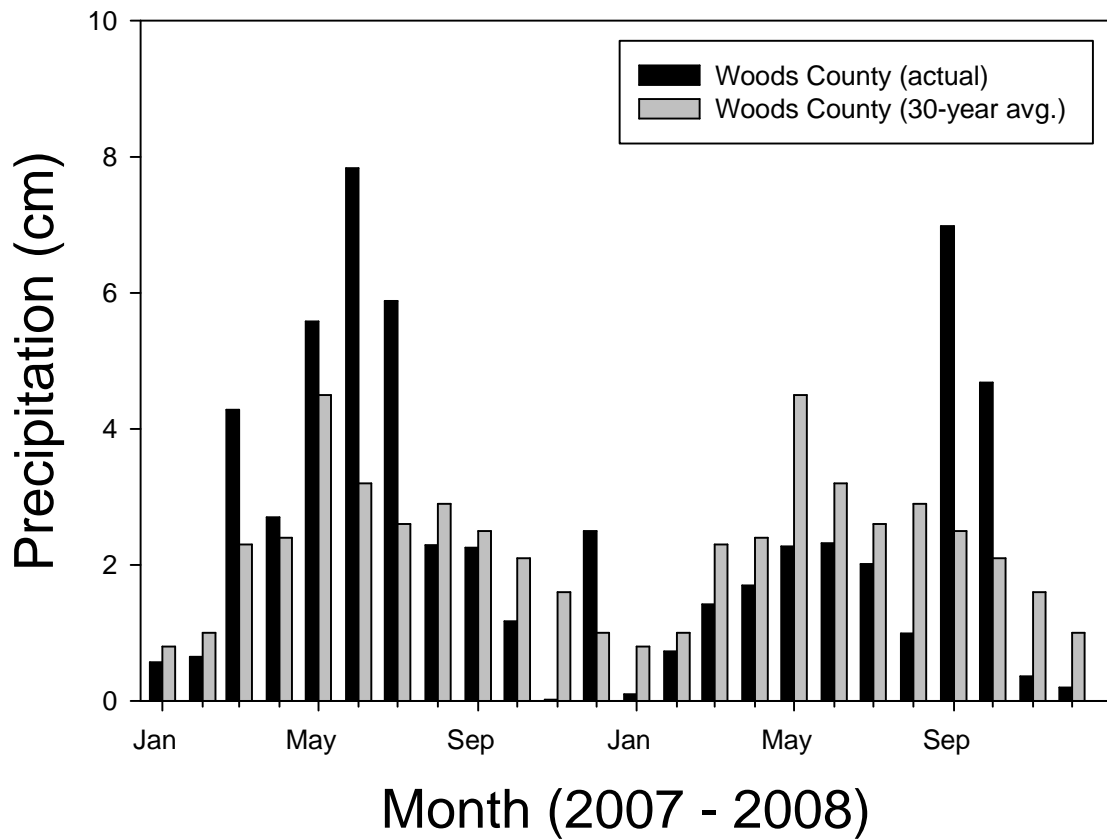


Figure 3.1. Monthly precipitation trends on shrub establishment sites (36°35'9" N, 98°46'54") compared to the 30-year average in Woods County, Oklahoma, 2007 – 2008.

Treatments

Forty establishment plots (6 m diameter) were planted on two sites on 14 – 16 March 2007 prior to Chickasaw plum bud break. Ten Chickasaw plum plots and five each of smooth sumac and fragrant sumac were planted at Site 1-2007 and Site 2-2007. Plots were spaced at 30-m intervals. A dibble bar was used to plant all stems on 60- cm- ×- 60 -cm spacing.

For the plum planted at Site 1 and 2, three different propagules (20 each) were planted alternately in each of the ten plots per site. Plum BRS obtained from the Oklahoma Forestry Services seedling nursery in Goldsby, Oklahoma, were compared to locally adapted transplants collected on site that were coppiced (CT) or left intact (IT). Bare-root seedlings were 1 year old and had all been top pruned at the nursery to a height of 20 cm. These propagules were planted with the root collar at ground level and all initial heights were assumed to be 20 cm. Transplants were selected from the periphery of well-established local stands of plum. Transplants had initial diameters between 3 mm and 17 mm (average 7.5 mm) and IT had heights ranging from 17 cm to 104 cm (average 59 cm). All transplants had a lateral root ≥ 15 cm in length. Based on observation of annual growth rings of the CT propagules, the aboveground portions of the transplants were between 1 and 3 years old. Half of the plum transplants were coppiced, i.e., their tops were cut approximately 1 cm above ground line.

For the smooth sumac plots (five at Site 1, five at Site 2), only CT or IT were planted as I was unable to find a commercial seedling source from Oklahoma. Each plot contained 20 of each propagule type. Transplants were taken locally from areas within a

large stand of smooth sumac adjacent to Site 1-2007. Stem diameters ranged from 4 mm to 14 mm (average 8 mm) and IT had heights between 16 cm and 91 cm (average 47.5 cm).

All transplants were obtained using a narrow shovel to sever the roots and extract ramets. The transplants were moved to the plots in buckets filled with water. For fragrant sumac, only BRS (Oklahoma Division of Forestry seedling nursery, Goldsby, Oklahoma) were used because of the difficulty transplanting locally obtained ramets of this species. Each of 10 plots (five at Site 1, five at Site 2) contained 36 BRS.

Site preparation treatments included competition control and tillage. In February 2007, half of each plot was tilled to a depth of about 15 cm using a 1.5-m-wide disk harrow pulled by a tractor. Several passes were made to ensure uprooting of existing vegetation. Perpendicular to the tillage treatment, 0.15 kg ha⁻¹ sulfometuron methyl (Oust, DuPont, Wilmington, DE) was sprayed on March 5 to eliminate competition from grasses and forbs on half of each plot. Oust is a pre-emergent herbicide commonly used in forestry for site preparation. A solution of 1% glyphosate (RoundUp, Monsanto, Creve Coeur, MO) was used to spot treat the plots twice during the 2007 growing season.

Based on results from the 2007 study, 36 additional plots were planted in 2008 to test the effects of competition control using weed cloth, timing of planting, and propagule type (CT vs. BRS for plum). Transplants were collected in the same manner as the 2007 planting. All bare-root seedlings were obtained from the Oklahoma Forestry Services Forest Regeneration Center. Half of each 6-m-diameter plot was covered with 15 mil, 83g m⁻² Polyscape weed barrier cloth (Shaw Fabrics Products, Wellington, CO) as a

physical barrier and alternative to chemical competition control. Twelve plots each were planted (six plum, three smooth sumac, three fragrant sumac) on 4 February, 26 February, and 18 March 2008. Chickasaw plum plots contained a total of 60 propagules, half of which were BRS and half of which were CT pruned 20 cm above ground line. Smooth sumac plots contained 40 stems that consisted entirely of IT. Fragrant sumac plots contained 36 BRS.

Measurements and Experimental Design – 2007 Planting

Survival was recorded seven times throughout 2007 and 2008 (Fig. 3.2). Ground line diameters and total heights were measured on surviving stems before and after each growing season. Heights were initially set at 20 cm for BRS because of nursery pruning. Coppiced transplants were cut at ground level and initial heights were set at 0 cm. Diameter measurements after the first and second growing seasons were always made on the largest living stem. Heights were measured to the tallest living portion of the stem. First year, second year, and total diameter and height increment were calculated by taking the difference between each living stem's diameter or height during sequential dormant seasons. Height and diameter increment do not reflect growth for the CT and IT propagules. Initial diameter measurements were taken on the main stem of transplanted propagules. Subsequent sprouting from the stem collar or root of the coppiced transplants as well as occasional mortality of the main stem and resprouting of the intact transplants confounded estimates of diameter growth. Likewise, frequent partial mortality of the main stem of the IT transplants confounded estimates of height growth. While irrelevant as estimates of growth for the transplant treatments, height and diameter

measurements and associated increments serve as important estimates of the potential rate of stand development that might be expected when planting different propagules.

Due to morality in the herbicide treatment, this factor was dropped from all analyses. The variables propagule source and tillage were tested for each of the three species separately. Within each plot, the stems of each propagule type \times tillage combination were averaged and the mean served as the experimental unit. For plum and smooth sumac, differences between the tillage and propagule treatments were tested using a split-plot ANOVA. Sites served as blocking variables. Tillage was the whole-plot factor and propagule type was the split-plot factor. For fragrant sumac only BRS were planted and tillage effects were tested using a randomized complete block design.

Measurements and Experimental Design – 2008 Planting

Survival was documented on 15 May, 11 July, and 18 September 2008. Initial measurements of stem heights and diameters were taken on all of the plants before the propagules initiated growth. Subsequent measurements were taken on surviving stems during the following dormant season as described above. Height and diameter increments were calculated by taking the difference between initial and final heights and diameters.

For the 2008 study, stems of the same propagule \times weed cloth combination within plots were averaged to obtain the experimental unit. For Chickasaw plum, planting date served as the whole-plot factor, competition control served as the first split-plot factor, and propagule type as the second split-plot factor. For the two sumac species, planting date served as the whole plot factor and competition control as the split-plot factor.

While the effects of planting date were tested, differences cannot be definitively ascribed to seasonal differences since only one planting event per time period could be included in a 1- year study.

RESULTS

2007 Planting

Tillage Effects. Tillage did not have a large or consistent effect on survival, diameter increment, or height increment. At the end of the two growing seasons, means for the tilled and untilled treatments for plum were $45 \pm 3.3\%$ SE and $44 \pm 2.9\%$ SE for survival ($P = 0.82$), 16.9 ± 1.59 cm SE and 17.7 ± 2.18 cm SE for height increment ($P = 0.99$), and 0.70 ± 0.423 mm and 1.30 ± 0.225 mm for diameter increment ($P = 0.28$) ($n = 20$). For smooth sumac after 2 years, survival was $49 \pm 7.5\%$ SE and $49 \pm 7.3\%$ SE and height increment was 6.6 ± 1.64 cm SE and 7.4 ± 2.18 cm SE ($P = 0.64$) for the tilled and untilled treatments respectively ($n = 10$). Tillage decreased diameter increment of smooth sumac over the first 2 years from -0.43 ± 0.223 mm SE to -1.29 ± 0.335 mm SE ($n = 10$, $P = 0.04$). For fragrant sumac over the first two growing seasons, means for the tilled and untilled treatments were $77 \pm 10.4\%$ SE and $88 \pm 8.9\%$ SE ($n = 10$) for survival ($P = 0.27$), 8.7 ± 1.57 cm SE and 10.6 ± 1.03 cm SE for height increment ($P = 0.47$), and 0.88 ± 0.470 mm SE mm and 0.88 ± 0.141 mm SE for diameter increment. Because of the lack of a strong tillage response, only the main effects of propagule type are presented and discussed below.

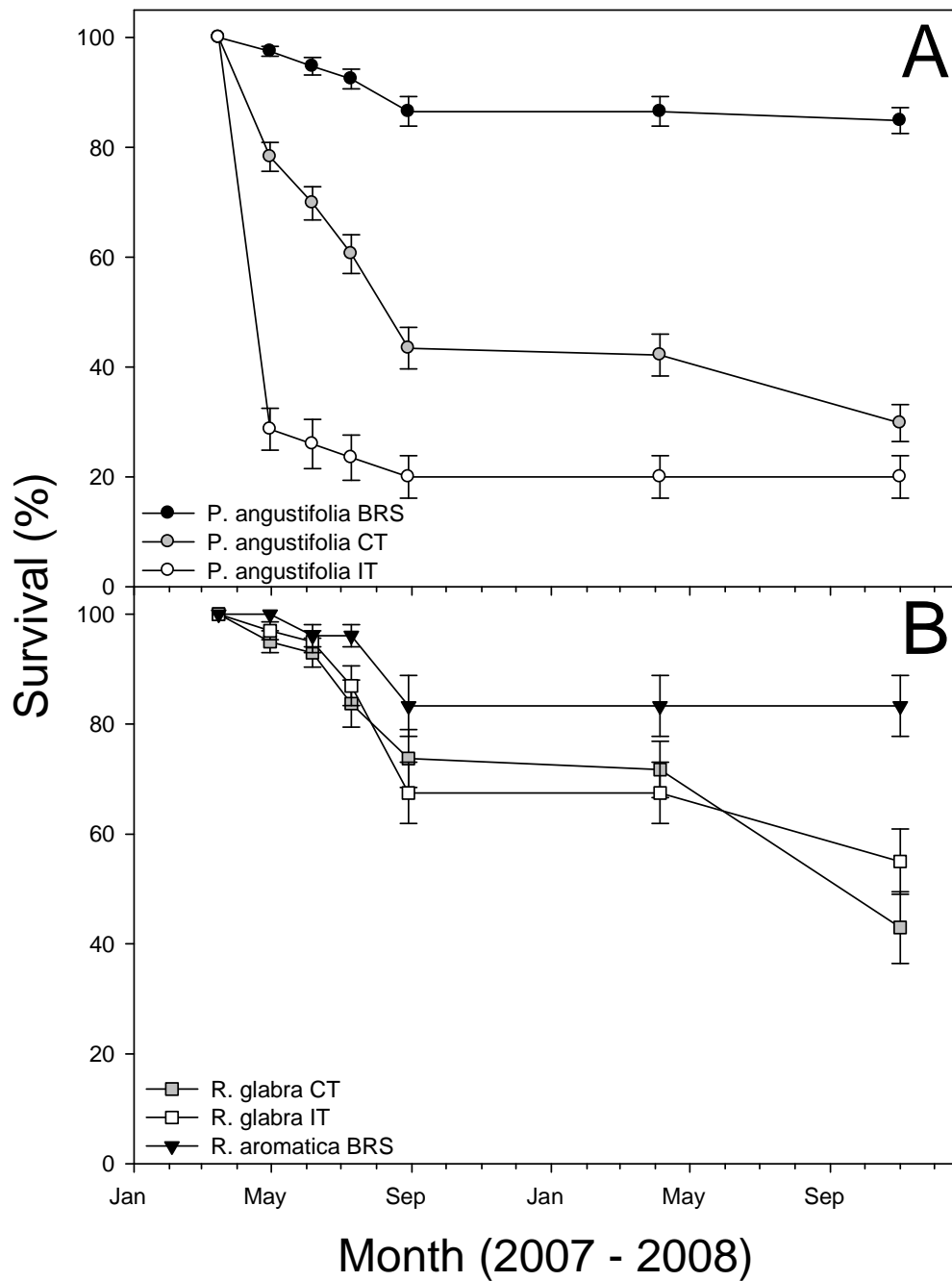


Figure 3.2. Trends in survival \pm 1 SE (%) of shrub propagules planted in Woods County, Oklahoma, 2007 – 2008. **A**, Chickasaw plum propagules ($n = 40$). **B**, sumac propagules ($n = 20$). BRS indicates bare-root seedlings; CT, coppiced transplants; and IT, intact transplants.

Chickasaw Plum. After two growing seasons, survival of BRS (85%) was greater than that of the transplants. Among transplants, coppicing increased survival of plum from 20 to 30% when measured after two years. (Fig. 3.2). The pattern of survival over the second growing season varied among propagules. Survival of coppiced transplants decreased from 40 to 30% during the second growing season while most individuals in the BRS and IT treatments that survived the first growing season survived the second as well. Initial diameters of BRS propagules ranged from 3 – 11 mm with some individuals from all size classes surviving. No individuals from the CT treatment with an initial diameter >13 mm survived (initial diameter range of 3 – 15 mm) and no individuals from the IT treatment with an initial diameter >10 mm survived (initial diameter range of 3 – 17).

Initial mean diameters were greater for the transplants than for the BRS (Table 3.1). However, by the end of the second growing season, diameters of surviving individuals were largest for the BRS propagules because diameter increment was greatest in this treatment for both years ($p < 0.0001$). Initial heights were dependent on propagule type and whether the propagule had been pruned or coppiced. During the first two growing seasons, height increment varied by propagule ($p < 0.0001$) such that total height after two years was similar among the BRS and IT treatments and lowest in the CT treatment (Table 3.2).

Table 3.1. Mean (± 1 SE) annual diameter and diameter increment after 2 years for shrub propagules on Sites 1 and 2 in Woods County, Oklahoma, 2007 – 2008.

| Species | Propagule ¹ | <i>n</i> | Diameter (mm) | | | Diameter Increment (mm) | | |
|----------------|------------------------|----------|---------------|---------------|---------------|-------------------------|----------------------|----------------|
| | | | Initial | Year 1 | Year 2 | 1 st Year | 2 nd Year | Total |
| Chickasaw plum | BRS | 40 | 5.9 \pm 0.1 | 6.0 \pm 0.1 | 8.7 \pm 0.3 | 0.1 \pm 0.1 | 2.7 \pm 0.3 | 2.8 \pm 0.3 |
| | CT | 40 | 7.6 \pm 0.2 | 4.1 \pm 0.3 | 6.0 \pm 0.3 | -3.6 \pm 0.5 | 2.2 \pm 0.4 | -1.5 \pm 0.4 |
| | IT | 40 | 7.4 \pm 0.2 | 5.6 \pm 0.3 | 7.2 \pm 0.3 | -0.3 \pm 0.3 | 1.5 \pm 0.3 | 1.2 \pm 0.3 |
| Smooth sumac | CT | 20 | 8.5 \pm 0.2 | 5.5 \pm 0.2 | 6.9 \pm 0.3 | -3.1 \pm 0.2 | 0.9 \pm 0.5 | -2.3 \pm 0.5 |
| | IT | 20 | 8.5 \pm 0.2 | 8.7 \pm 0.2 | 9.1 \pm 0.3 | 0.3 \pm 0.1 | 0.1 \pm 0.3 | 0.4 \pm 0.3 |
| Fragrant sumac | BRS | 20 | 6.1 \pm 0.2 | 6.4 \pm 0.3 | 7.3 \pm 0.4 | 0.0 \pm 0.1 | 1.3 \pm 0.2 | 0.9 \pm 0.3 |

¹BRS indicates bare-root seedlings; CT, coppiced transplant; IT, intact transplant.

Table 3.2. Mean (± 1 SE) annual height and height increment after 2 years for shrub propagules on Sites 1 and 2 in Woods County, Oklahoma, 2007 – 2008.

| Species | Propagule ¹ | <i>n</i> | Height (cm) | | | Height Increment (cm) | | |
|----------------|------------------------|----------|----------------|----------------|----------------|-----------------------|----------------------|----------------|
| | | | Initial | Year 1 | Year 2 | 1 st Year | 2 nd Year | Total |
| Chickasaw plum | BRS | 40 | 20.0 \pm 0.0 | 34.3 \pm 0.9 | 43.4 \pm 1.3 | 14.3 \pm 0.9 | 9.2 \pm 1.1 | 23.4 \pm 1.3 |
| | CT | 40 | 0.0 \pm 0.0 | 18.5 \pm 1.3 | 26.2 \pm 1.5 | 18.5 \pm 1.3 | 7.9 \pm 1.5 | 26.2 \pm 1.5 |
| | IT | 40 | 59.0 \pm 1.3 | 48.6 \pm 3.0 | 45.2 \pm 2.4 | -3.8 \pm 2.3 | -1.8 \pm 1.1 | -5.9 \pm 1.6 |
| Smooth sumac | CT | 20 | 0.0 \pm 0.0 | 11.0 \pm 0.9 | 20.5 \pm 2.4 | 11.0 \pm 0.9 | 8.9 \pm 1.5 | 20.5 \pm 2.4 |
| | IT | 20 | 48.7 \pm 1.9 | 45.8 \pm 2.1 | 44.8 \pm 1.8 | -2.7 \pm 0.5 | -1.9 \pm 0.8 | -4.5 \pm 1.0 |
| Fragrant sumac | BRS | 20 | 20.0 \pm 0.0 | 25.8 \pm 0.9 | 29.7 \pm 1.3 | 5.8 \pm 0.9 | 4.6 \pm 0.9 | 9.7 \pm 1.3 |

¹BRS indicates bare-root seedlings; CT, coppiced transplant; IT, intact transplant.

Smooth Sumac. Survival after 2 years was similar for coppiced and intact transplants ($P = 0.17$, Fig. 3.2). No transplants <5 mm initial diameter survived (initial diameter range 4 – 13 mm). The average initial diameter for sumac transplants was 8.5 mm. After two growing seasons mean diameter increment of the CT treatment was negative due to mortality of the initial ramet and basal resprouting. As a result, the IT treatment had a mean diameter 32% greater than the CT treatment after two years (Table 3.1). The mean height of the IT treatment was negative due to frequent die-back of portions of the main ramet. However, total height after two years was almost twice as tall in the IT as in the CT treatment due to the greater initial height of the intact transplants (Table 3.2).

Fragrant Sumac. Eighty-three percent of the fragrant sumac BRS survived after 2 years (Fig. 3.2). Seedlings from all size classes survived (initial diameter range 3 – 11 mm). There was <1 mm diameter increment (Table 3.1) during the first two growing seasons but nearly 10 cm in height increment (Table 3.2).

2008 Planting

Chickasaw plum. Overall, survival of plum BRS propagules was greater than for CT propagules, i.e., 77 and 29% respectively (Table 3.3). However, there was an interaction between planting date and propagule type ($P = 0.004$) because BRS survival was fairly consistent across planting dates (76, 75, and 80% survival for successively later planting dates, $P = 0.56$) while survival of CT increased with later planting dates

(16, 21, 52% survival for successively later planting dates, $P = 0.03$). The application of weed cloth increased ($P = 0.005$) survival compared to no cloth from 47 to 60%.

Diameter increment after 1 year of individuals planted on the early, middle, and late planting dates was 0.5 mm, 1.2 mm, and 0.7 mm, respectively (Table 3.3, $P = 0.002$). Diameter increment of individuals in the BRS treatment (1.1 mm) were greater than those in the CT treatment (0.4 mm) ($P = 0.003$). Compared to no weed cloth, weed cloth increased diameter increment from 0.6 to 1.0 mm ($P = 0.005$) in the 2008 growing season.

Height increments for plum planted on the early, middle, and late planting dates were 0.6 cm, 3.0 cm, and 0.4 cm (Table 3.3, $P = 0.008$), respectively. However, height increment was similar for the first and second planting dates for the weed cloth treatment (2.0, 2.3, and 0.6 cm for successively later planting dates) but was greatest for the middle planting date for the no weed cloth treatment (-1.4, 4.2, 0.3 cm for successively later planting dates) resulting in an interaction between planting date and the weed cloth treatment ($P = 0.02$). . There also was an interaction between planting date and propagule type ($P = 0.02$) because height increment of BRS was fairly consistent across planting dates (1.4, 2.3, and 1.8 cm between successively later dates) while height increment of CT varied considerably (-1.3, 3.7, -1.0 between successively later planting dates).

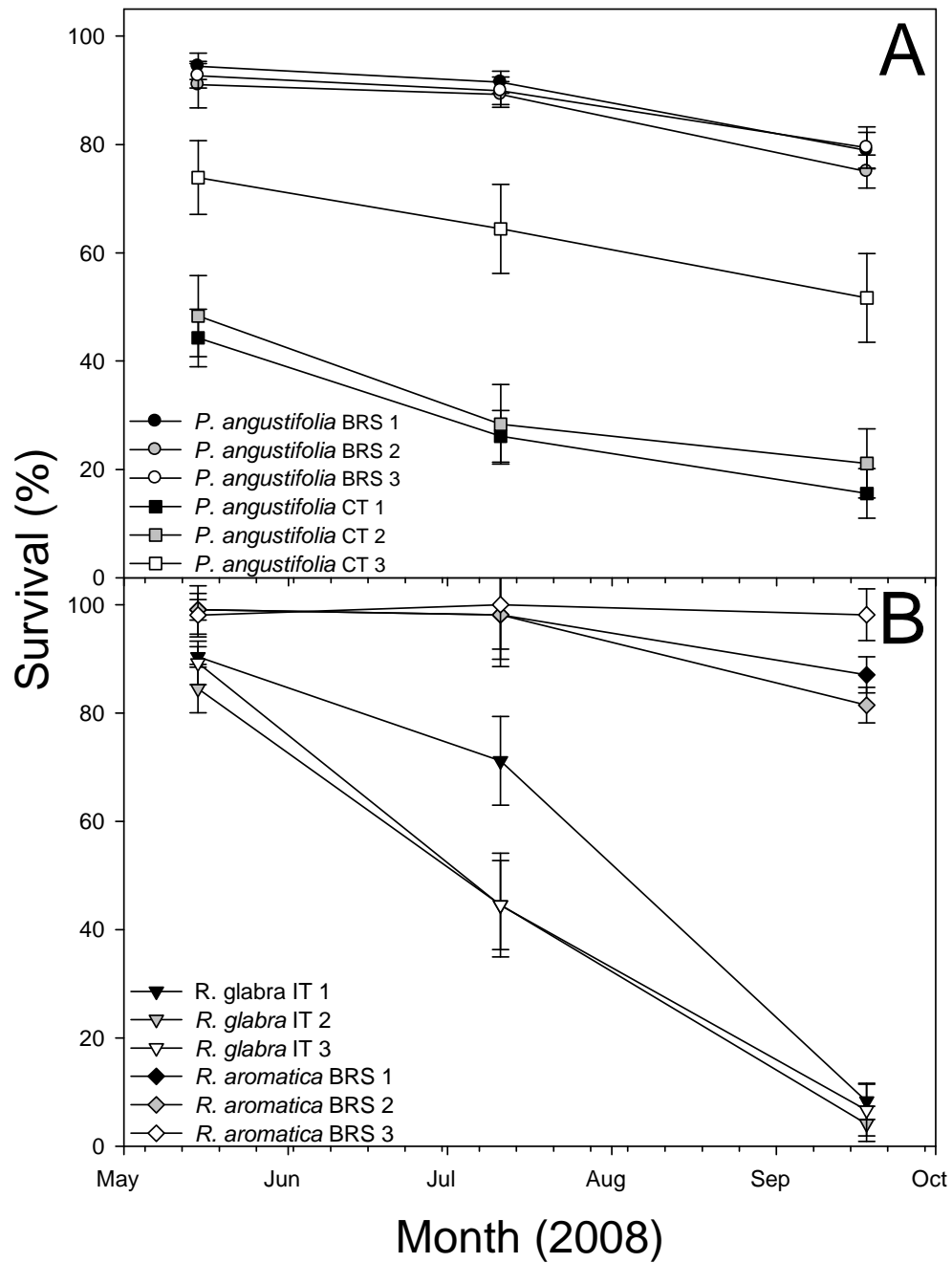


Figure 3.3. Trends in survival \pm 1 SE (%) of shrub propagules planted in Woods County, Oklahoma, 2008. **A**, Chickasaw plum propagules ($n = 6$). **B**, sumac propagules ($n = 3$). BRS indicates bare-root seedlings; CT, coppiced transplants; IT, intact transplants; 1, propagules planted 4 February; 2, propagules planted on 26 February; and 3, propagules planted on 18 March.

Table 3.3. Survival and growth means after 2 years (± 1 SE) for Chickasaw plum propagules planted in Woods County, Oklahoma, 2008 ($n = 6$).

| Planting Date | Weedcloth | ¹ Propagule | Survival (%) | Diameter (mm) | | | Height (cm) | | |
|---------------|-----------|------------------------|--------------|---------------|---------------|---------------|----------------|----------------|----------------|
| | | | | Initial | Final | Increment | Initial | Final | Increment |
| 4 February | Cloth | BRS | 80 \pm 4 | 5.1 \pm 0.4 | 6.1 \pm 0.4 | 1.1 \pm 0.3 | 23.1 \pm 1.2 | 24.7 \pm 0.9 | 2.6 \pm 1.0 |
| | | CT | 23 \pm 8 | 6.0 \pm 0.5 | 5.1 \pm 0.7 | 0.2 \pm 0.3 | 21.5 \pm 3.2 | 20.4 \pm 2.4 | 1.3 \pm 1.1 |
| | No Cloth | BRS | 72 \pm 5 | 5.0 \pm 0.3 | 5.5 \pm 0.2 | 0.4 \pm 0.0 | 22.0 \pm 1.3 | 22.6 \pm 0.9 | 1.2 \pm 0.7 |
| | | CT | 8 \pm 3 | 6.1 \pm 0.3 | 4.3 \pm 0.7 | 0.1 \pm 0.1 | 18.2 \pm 1.3 | 19.7 \pm 1.3 | -3.9 \pm 2.4 |
| 26 February | Cloth | BRS | 81 \pm 4 | 3.7 \pm 0.3 | 5.6 \pm 0.3 | 1.9 \pm 0.2 | 22.6 \pm 1.1 | 23.0 \pm 1.1 | 2.4 \pm 0.6 |
| | | CT | 28 \pm 9 | 5.7 \pm 0.3 | 6.1 \pm 0.5 | 0.8 \pm 0.2 | 22.4 \pm 1.4 | 21.5 \pm 1.6 | 2.1 \pm 1.2 |
| | No Cloth | BRS | 69 \pm 4 | 4.1 \pm 0.2 | 5.0 \pm 0.3 | 1.2 \pm 0.1 | 24.9 \pm 0.7 | 25.5 \pm 0.8 | 3.1 \pm 0.7 |
| | | CT | 14 \pm 8 | 5.8 \pm 0.5 | 6.2 \pm 1.3 | 0.7 \pm 0.3 | 23.8 \pm 1.9 | 28.0 \pm 2.5 | 5.2 \pm 1.0 |
| 18 March | Cloth | BRS | 83 \pm 8 | 4.5 \pm 0.5 | 5.7 \pm 0.6 | 1.1 \pm 0.2 | 20.5 \pm 0.8 | 22.9 \pm 1.3 | 1.8 \pm 0.7 |
| | | CT | 62 \pm 13 | 5.9 \pm 0.2 | 6.8 \pm 0.6 | 0.7 \pm 0.4 | 21.2 \pm 1.1 | 20.2 \pm 1.2 | -0.7 \pm 0.5 |
| | No Cloth | BRS | 77 \pm 3 | 5.6 \pm 0.3 | 6.5 \pm 0.3 | 0.9 \pm 0.2 | 23.7 \pm 0.6 | 25.1 \pm 1.1 | 1.8 \pm 0.8 |
| | | CT | 41 \pm 9 | 5.5 \pm 0.2 | 6.1 \pm 0.4 | 0.1 \pm 0.2 | 20.6 \pm 1.0 | 19.0 \pm 0.9 | -1.3 \pm 0.7 |

¹BRS indicates bare-root seedlings; CT, coppiced transplant; IT, intact transplant.

Smooth sumac. In the 2008 planting, smooth sumac exhibited poor survival regardless of planting date with 8, 3, and 7% survival rates for the early, middle, and late planting dates respectively ($P = 0.72$, Table 3.4). The weed cloth and no weed cloth treatments had survival rates of 2% and 10% respectively ($P = 0.06$). Statistical analyses for height and diameter increment could not be reliably conducted because four of nine plots did not have any individuals that survived until the end of the first growing season.

Table 3.4. Survival and growth means after 2 years (± 1 SE) for smooth sumac intact transplants planted in Woods County, Oklahoma, 2008 ($n = 3$).

| Planting Date | Weedcloth | Survival (%) | Diameter (mm) | | | Height (cm) | | |
|---------------|-----------|--------------|---------------|-----------------|---------------|----------------|----------------|----------------|
| | | | Initial | Final | Increment | Initial | Final | Increment |
| 4 February | Cloth | 5 ± 3 | 7.0 ± 0.1 | 8.5 ± 0.5 | 1.8 ± 2.3 | 37.7 ± 2.1 | 35.5 ± 6.5 | -3.5 ± 3.5 |
| | No Cloth | 12 ± 6 | 7.7 ± 0.1 | 7.5 ± 0.2 | 0.0 ± 0.0 | 34.3 ± 4.8 | 28.8 ± 1.8 | -1.7 ± 2.0 |
| 26 February | Cloth | 0 ± 0 | 7.2 ± 0.3 | ND ¹ | ND | 45.3 ± 3.0 | ND | ND |
| | No Cloth | 5 ± 5 | 7.7 ± 0.2 | 6.7 | 0.3 | 41.9 ± 2.6 | 30.3 | -11.0 |
| 18 March | Cloth | 2 ± 2 | 7.2 ± 0.3 | 8.0 | 0.0 | 50.7 ± 3.4 | 23.0 | -11.0 |
| | No Cloth | 12 ± 9 | 6.6 ± 0.2 | 6.5 ± 0.5 | 0.2 ± 0.2 | 40.7 ± 3.1 | 28.1 ± 3.1 | -3.1 ± 2.1 |

¹ND indicates when no data were available due to mortality.

Fragrant Sumac. Fragrant sumac BRS exhibited good survival regardless of when they were planted with 86, 83, and 98% survival at the end of the first growing season, for the early, middle, and late planting dates ($P = 0.08$, Table 3.5). Fragrant sumac survival was not significantly different with or without weed cloth (91 and 87% respectively, $P = 0.54$). Diameter increment averaged 0.7 mm and did not differ significantly with planting date or weed cloth (Table 3.5). However, diameter increment was greatest for the first planting date with the weed cloth treatment (1.0, 0.5, and 0.6 mm with successive planting dates) but greatest for the second planting date with no weed cloth treatment (0.4, 1.0, and 0.4 mm with successive planting dates) resulting in an interaction between planting date and weed cloth treatment ($P = 0.04$). Weed cloth decreased height increment ($P = 0.05$) compared to no cloth (-2.6 and -1.7 cm respectively).

Table 3.5. Survival and growth means after 2 years (± 1 SE) for fragrant sumac bare-root seedlings planted in Woods County, Oklahoma, 2008 ($n = 3$).

| Planting Date | Weedcloth | Survival (%) | Diameter (mm) | | | Height (cm) | | |
|---------------|-----------|--------------|---------------|---------------|---------------|----------------|----------------|----------------|
| | | | Initial | Final | Growth | Initial | Final | Growth |
| 4 February | Cloth | 87 ± 4 | 4.6 ± 0.6 | 5.6 ± 0.6 | 1.0 ± 0.1 | 24.4 ± 1.4 | 21.1 ± 0.8 | -2.4 ± 1.1 |
| | No Cloth | 85 ± 4 | 4.7 ± 0.0 | 5.2 ± 0.1 | 0.4 ± 0.0 | 23.4 ± 0.6 | 20.7 ± 1.2 | -1.9 ± 1.4 |
| 26 February | Cloth | 89 ± 3 | 4.3 ± 0.2 | 4.8 ± 0.2 | 0.5 ± 0.1 | 23.3 ± 0.5 | 19.7 ± 0.7 | -2.9 ± 1.3 |
| | No Cloth | 76 ± 13 | 4.4 ± 0.5 | 5.5 ± 0.4 | 1.0 ± 0.3 | 23.6 ± 1.9 | 23.0 ± 2.2 | -0.3 ± 0.8 |
| 18 March | Cloth | 96 ± 4 | 4.9 ± 0.3 | 5.6 ± 0.0 | 0.6 ± 0.2 | 21.6 ± 1.3 | 19.1 ± 1.1 | -2.6 ± 0.2 |
| | No Cloth | 100 ± 0 | 4.6 ± 0.4 | 5.0 ± 0.3 | 0.4 ± 0.2 | 21.9 ± 0.7 | 18.8 ± 1.0 | -3.0 ± 0.4 |

DISCUSSION

Cultural Treatments

In my study on deep sandy soils in northwestern Oklahoma, tillage did not have a positive effect on survival or growth on the three species tested. This finding differs from the more typical positive response of seedling survival and growth to tillage. Carlson *et al.* (2006) found that tillage had a positive effect on survival of loblolly pine (*Pinus taeda* L.) seedlings on some Piedmont sites across the southeastern United States. Tillage improved height and diameter growth of loblolly pine seedlings on the Upper Coastal Plain and Piedmont of Georgia on a wide range of soil types (Wheeler et al. 2002; Lincoln et al. 2007). Karlsson (2002) showed that silver birch (*Betula pendula* Roth) seedlings had increased survival on sandy soils with deep plowing. On upland sites, tillage increased growth primarily by increasing the penetration ability of roots (Will et al. 2002). The failure to find a tillage effect in the current study indicates that either root penetration does not limit growth rate of Chickasaw plum, smooth sumac, or fragrant sumac in northwestern Oklahoma or that tillage treatments did not have a lasting effect on soil properties. In either case, it does not appear that tillage is necessary for establishment of shrubs in sandy soils of northwestern Oklahoma.

Competition control increases growth by allowing desired plants to utilize site resources more completely (Smith et al. 1997). The herbicide used in this study, sulfometuron methyl, increased survival and growth of cottonwood (*Populus deltoides* Bartram ex Marsh.) seedlings compared to cultivation and physical barriers (Geyer et al. 2006). Sulfometuron methyl applied over longleaf pine (*P. palustris* Mill.) seedlings

increased diameter growth and the rate at which seedlings emerged from the grass stage (Ramsey and Jose 2004). However, competition control with the pre-emergent herbicide sulfometuron methyl is not appropriate for seedling and transplant establishment for the species tested in my study because of the complete mortality experienced in association with its application. In another study, sulfometuron methyl reduced hardwood regeneration growth except in combination with lime to increase soil pH (Schreffler and Sharpe 2003). The pH of the soils in this study is neutral or slightly acidic. Perhaps using a soil amendment to increase pH could have improved propagule survival and performance in the herbicide treatment, but given the relatively high pH of the soils already, the failure of the herbicide plots appears to be related to sensitivity of the shrub species. Application of a different herbicide that does not have a negative effect on plum or sumac would probably have beneficial effects on the establishment of shrubs and may warrant further research.

In my study, weed cloth increased survival of plum by 13% and diameter growth by 40%, but had little effect on the other species. In previous studies, weed cloth increased survival and growth of seedlings. For instance, weed cloth increased survival of cottonwood compared to other synthetic mulches (Geyer et al. 2006) and increased height growth for newly established Arizona cypress (*Cupressus arizonica* Greene) seedlings compared to no treatment in New Mexico (Harrington et al. 2005). Using weed cloth has several limitations. Installing weed cloth is cumbersome. Staples are used to secure the edges, but in northwestern Oklahoma where strong winds are common, the cloth must also be almost covered with soil to prevent the wind and animal traffic from shredding it. The fabric is made of plastic fibers that degrade and become brittle with

prolonged exposure to sunlight. The Polyscape weed barrier fabric costs about \$0.54 m⁻² and which cost approximately \$12 plot⁻¹ in my study.

Propagule Type

Bare-root seedlings of both plum and fragrant sumac had excellent survival rates (>80% after 2 years). The primary advantage seedlings have over transplants is their well established root system. Bare-root seedlings of common native species are generally easy to obtain from nurseries. The Oklahoma Forestry Services Forest Regeneration Center sells > 30 species for conservation and forestry purposes at a cost of \$0.05 – \$0.60 each. The plots were planted with 60 stems. If only seedlings had been planted each stand would have cost \$20. However, considering the high survival rates of BRS and the fact that a mature stand can arise from one seedling, a lower planting density might be operationally employed to reduce seedling costs. After only two years since planting, we cannot yet evaluate number of years it will take before the different propagules are large enough to provide suitable wildlife habitat.

Transplants may be a viable option if local sources are available. Ramets of Chickasaw plum and smooth sumac are relatively easy to collect and transport. However, fragrant sumac spreads predominately by basal sprouts and transplants could not be collected. Transplants should be taken in the dormant season prior to bud break. Coppicing the transplants removes most of the preformed buds which reduces initial leaf area and plant water use and decreases the likelihood of mortality from water stress during the first several months. In my study, coppicing transplants increased survival in Chickasaw plum but not smooth sumac. However, most of the surviving non-coppiced

sumac stems sprouted from the base indicating that there could be a physiological adaptation that is similar in function to coppicing that occurs when stems are severed from the mother plant. Despite the lower survival rates of transplanted stems, local sources are readily available and can be planted at higher densities than BRS to obtain the same number of surviving plants. Other potential advantages of transplants are the low cost and effort associated with storage, transportation, and planning as well as genetics that are adapted to local conditions.

Height and diameter increment could not serve as measurements of growth since they were confounded by top die-back and resprouting. Additionally, there was evidence of herbivory by deer, especially for smooth sumac, which reduced plant heights. These sprouting characteristics make growth estimates in year one indicate that initial size of transplants is no indication of plant size in the first several years. However, the measurements of height and diameter are important as they serve as estimates of the rate of stand establishment associated with different propagules and cultural treatments. Even though they suffered negative height increments after two growing seasons, the IT propagules were tallest due to greater initial height and may result in the most rapid stand establishment. Growth measurements in subsequent years will be relevant indicators of vigor and the trajectory of stand establishment.

Planting Date

Planting date had little effect on survival of BRS. This result is consistent with those for twelve tree species planted on multiple dates spanning the dormant season in Indiana

(Seifert et al. 2006). While differences between planting dates can be statistically tested, the differences cannot be unambiguously ascribed to late winter, early spring, or mid spring since these specific timings could only be replicated once in a 1-year study. However, planting late in spring just before bud break seemed to provide the best conditions for survival of Chickasaw plum transplants. This may be due to warming soil temperatures and spring rains encouraging immediate growth of newly planted transplants. Local measurements of precipitation indicate that all three planting dates had rainfall events shortly after or before planting (Fig. 3.5). It is doubtful that successive rainfall events had a cumulative effect on soil moisture because of the high permeability of these deep sands. However, the study site received heavy rain the day before the third planting which could have provided conditions that improved survival. Watering or irrigating newly severed transplants may facilitate dormant buds to produce roots sooner and allow for greater water uptake by existing roots. Another possibility related to better survival of transplants planted on the last date is that plant growth regulators active at the time of bud swelling allow these transplants to initiate root growth sooner. Additionally, the transplants taken on the last date were connected to the mother plant longer and could have received additional resources in preparation for resumption of aboveground growth (Boo and Pettit 1975).

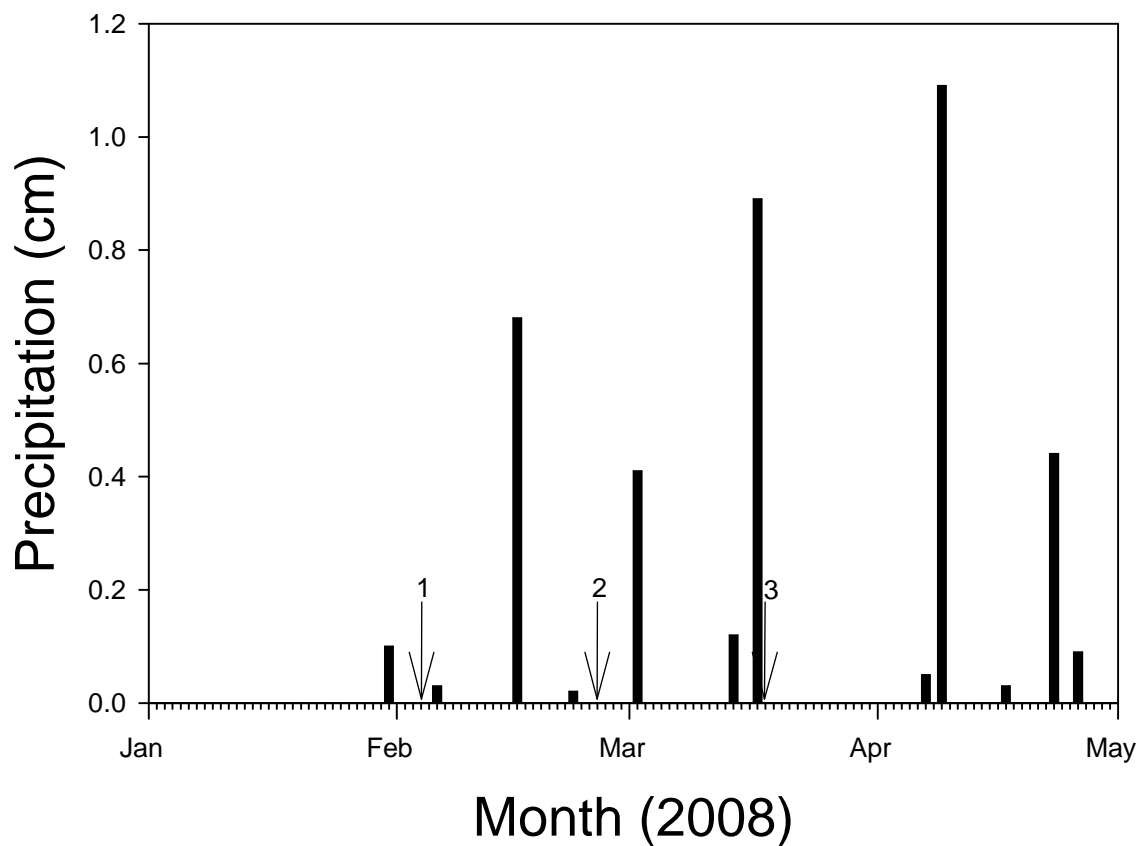


Figure 3.4. Local precipitation for Woods County, Oklahoma January to May 2008. Arrows indicate planting dates: 1, 4 February 2008; 2, 26 February 2008; and 3, 18 March 2008).

Conclusion

Establishing shrub clusters in grasslands of northwestern Oklahoma has the potential to improve habitat quality for species such as Northern Bobwhite. Minimal site preparation (mowing for access) was necessary for the species tested on the sandy soils used in these trials. Bare-root seedlings require less labor and had better survival rates than transplants. Long-term monitoring of these establishment stands is needed to give insight into the development of mature stands of Chickasaw plum, smooth sumac, and fragrant sumac.

CHAPTER IV

Early Independence of Interconnected Ramets in the Clonal Shrub Chickasaw Plum

ABSTRACT

Resource integration is a widespread phenomenon in clonal plants that allows for potential translocation of carbon and water between interconnected ramets. To better understand the importance of this process in Chickasaw plum (*Prunus angustifolia* Marsh.), growth (diameter and height), net photosynthesis (A_{net}), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), midday stem water potential (Ψ), and soil volumetric water content (VWC) of interconnected ramets were monitored during the 2008 growing season in Woods County, Oklahoma. I severed the roots between interconnected ramets on the interior (IS) and periphery (PS) of Chickasaw plum stands and left undisturbed control (IC and PC) plots for comparison. IS and IC plots measured the response of stems that were classified as a mother (Mo) or adjacent daughter (Ad) and the PS and PC plots focused on proximal (Px) and distal (Ds) stems. For all ramets, severing had little or no effect on growth, A_{net} , g_s , C_i , and VWC ($P \geq 0.18$). Though Chickasaw plum possesses persistent root connections between ramets there was minimal evidence of water or carbon resource integration between interconnected ramets under normal conditions.

Keywords

Prunus angustifolia, resource integration, root, sever, translocation

INTRODUCTION

Clonal plants have the potential to share resources, e.g., water, nutrients, and carbohydrates, between connected ramets (Evans 1988; deKroon et al. 1996; Alpert 1999; Herben 2004; Roiloa and Retuerto 2006). Obviously, a newly generated ramet receives resource subsidies from a mother plant during its genesis. However, it is unclear in many species the extent to which connected ramets continue to share resources.

Clonal plants have the ability to buffer the effects of resource heterogeneity on a small scale; i.e., the area occupied by interconnected clones (Herben 2004). Fertilizer was applied to largeleaf pennywort (*Hydrocotyle bonariensis* Comm. ex Lam.) clones and N integration among ramets and increased branching was observed illustrating this species' ability to exploit patchy resources across the landscape (Evans 1988). This trait may (Wijesinghe and Handel 1994) or may not (Peltzer 2002) increase the competitive ability of the plant. Addressing questions about the physiological processes dependent on the movement of water, carbon, and nutrient resources among ramets of clonal plants will help to better understand their ecological niche and competitive ability and will lead to more efficient management strategies.

Most research designed to measure movement of resources among clonal plants has focused on herbaceous plants because of the relative ease with which controlled experiments can be conducted (Eriksson 1993; Alpert 1999; Herben 2004; Zhang et al. 2008). Woody clonal plants pose problems for experimenters due to slow growth rates and large clone size. Generally studies on woody plants are conducted *in situ* and it is often difficult to eliminate confounding factors (Eriksson 1993).

Plants can be wounded (either roots or stems) to observe resource allocation among ramets after disturbance. The movement of carbon is inferred from the growth rate and location or density of new sprouts (Matlack 1997; Fraser et al. 2004; Gibson et al. 2004; Giudici and Zingg 2005). Boo and Pettit (1975) explored the root structure and carbohydrate reserves in shinnery oak (*Quercus havardii* Rydb.) and found that mechanical severing of ramets caused root carbon reserves in the remaining portion of the clone to decrease during early summer. This implied that carbohydrate reserves are transported to new or existing stems to aid in repair, maintenance, and renewal.

The goal of this study was to gain a better understanding of resource allocation in the clonal shrub Chickasaw plum (*Prunus angustifolia* Marsh.). Specifically, the aim was to determine the relative importance of persistent root connections and observe directionality in resource subsidies among ramets. The hypothesis that newly generated peripheral ramets rely on older portions of the genet for carbon or belowground resource subsidy was tested by measuring ramet growth, leaf gas exchange, and xylem water potential. Alternatively, older portions of the genet may rely on new ramets to gather resources from a previously unexploited space, or each ramet could be functionally independent shortly after it is generated.

METHODS

Study Area

This experiment was installed in early spring before the 2008 growing season. The study site was a native bluestem prairie community with soils that are deep loamy fine sands classified in the Eda series near Waynoka, Oklahoma (Woods County, N 36.52, W - 98.70). These soils are excessively drained thermic lamellic ustipsamments and are located on undulating dunes on alluvial plains (USDA-NRCS 2008). The plant community was dominated by little bluestem (*Schizachyrium scoparium* Michx.) with intermixed stands of Chickasaw plum. The primary land uses of this property were cattle grazing and hunting. The 30-year average annual precipitation for Woods County is 68 cm (Oklahoma Climatological Society, 2009). Local precipitation was measured and total rainfall in the area was 91 cm in 2007 and 60 cm in 2008. Temperature extremes ranged from -18 to 42 C in 2008.

Treatments

Fifteen Chickasaw plum stands that appeared to be undisturbed were used for this experiment. Stand diameters were approximately 7-15 m and representative for this species. An undisturbed plum clone resembles a hill in silhouette. There is a mother stem generated by a seed near the center of the stand. I presumed, within a stand, the stem with the greatest height and diameter was the mother based on a previous study on

Chickasaw plum that found a linear relationship between stem diameter and age (Dunkin et al. 2008) and other studies of clonal shrubs that identified age and size structure of clonal clusters (Gilbert 1966; Reinartz and Popp 1987). The mother trees in this study ranged from 2 – 3 m tall with diameters that ranged from 43 – 77 mm. Ramets get progressively smaller with distance from the mother. The 15 genets were randomly assigned one of the following treatments: interior sever (IS), peripheral sever (PS), and controls (IC and PC). For IS stands, the mother stem was identified and all connections to adjacent ramets were severed to a depth of at least 60 cm with a Toro Dingo trencher with a 10-cm-wide blade (Bloomington, MN). Three cuts were made to form a triangle around the mother (Fig. 4.1). Exploratory excavations indicated that connections between ramets were within 30 cm of the soil surface. The mother stems (Mo) and six adjacent stems (Ad) were tagged and height and diameter measurements recorded through the 2008 growing season to calculate ramet growth. For PS stands, the smallest stems on the periphery of the clone were located and severed from the clone using the trencher (Fig. 4.1). Six stems on the proximal (Px) and the six adjacent stems on the distal side (Ds) of the trench were monitored as described above. The five C plots were left unaltered and served as controls for both treatments. In IC and PC stands, stems were classified and measured using the same hierarchy as the sever treatments.

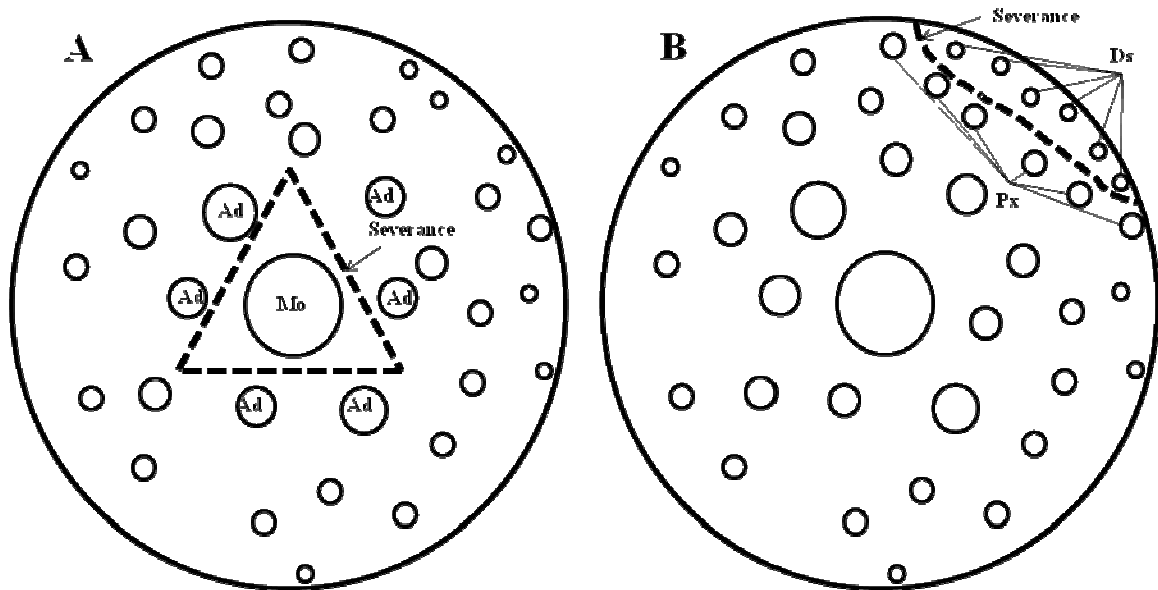


Figure 4.1. Diagram illustrating the general layout for interior (left) and peripheral (right) severing treatments, Woods County, Oklahoma, 2008. Stand area, density, and stem sizes are not to scale. **A**, interior severing treatment. **B**, peripheral severing treatment. Mo indicates mother stems; Ad, those adjacent to mothers; Px, stems on the proximal side of the peripheral severing treatment; and Ds, stems on the distal side of the peripheral severing treatment.

Measurements

Stem height was recorded for all ramets to the nearest 1 cm with a height pole. Stem diameter at ground level was recorded to the nearest 1 mm with dial calipers. Initial measurements were taken on 4 April 2008 with follow-up measurements on 22 January 2009. Diameter growth was calculated as the difference between the final diameter and the initial diameter. Height growth was calculated as the difference between the final height and the initial height.

Net photosynthesis (A_{net}), stomatal conductance to water vapor (g_s), intercellular CO_2 concentration (C_i), midday xylem water potential (Ψ), and soil volumetric water content (VWC) were measured five times (approximately every month) between April and August. Data were collected between 8:30 AM and 4:00 PM. For the interior treatment, Mo and Ad stems were measured. For the peripheral treatment, Px and Ds stems were measured. Leaf-level A_{net} , g_s , and C_i were measured with a LI-6400 portable photosynthesis system (Li-Cor Biosciences, Lincoln, NE). Light level was maintained at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ using the attached blue/red LED light source. The reference CO_2 was set to $400 \mu\text{mol mol}^{-1}$. One leaf from each plant on each sampling date was measured. Since leaves fit entirely into the cuvette, they were collected, placed in plastic bags, and kept refrigerated until leaf area was measured using the LI-3100 area meter (Li-Cor Biosciences, Lincoln, NE). Gas exchange measurements were recalculated using the actual leaf area measured. Midday xylem water potential (Ψ) was measured with a pressure chamber on one twig per stem (Portable Plant Water Status Console; SoilMoisture Corp., Santa Barbara, CA). Readings were taken at the moment sap was seen wetting the surface of the cut stem. Soil VWC was determined by time domain

reflectometry with the miniTrase kit (SoilMoisture Corp., Santa Barbara, CA) using the 30-cm waveguides and 10-ns pulse in the soil directly under measured stems.

Within the plots, stems from locations containing multiple measurements, i.e., positions Ad, Px, and Ds, were averaged and the average served as the experimental unit. As differences in growth and physiology related solely to position within the clone were expected, responses of severed ramets were compared to ramets of the same position from the unsevered control. The fifteen plots were assigned to five replicates based on proximity to one another. Two separate analyses were conducted, one that compared the effects of severing on Mo and Ad stems in the IS and IC treatments and another that compared the effects of severing on Px and Ds stems in the PS and PC treatment. A split-split-plot analysis was conducted to test the effects of severing treatment (whole-plot), ramet location (first split-plot factor), and date (second split-plot factor) as well as interactions. The factor of most interest was the interaction between severing treatment and stem position which tested whether the measured responses of stems in a given location differed depending on whether it was severed or not.

RESULTS

Diameter and height growth were similar among severed and unsevered stems of the same position for the comparison between the mother and adjacent stems (interaction between the severing treatment and ramet location for diameter growth $P = 0.41$ and height growth $P = 0.38$, Fig. 4.2, 4.3). Initial diameters of the IS and IC plots were 47.5

and 42.5 mm, respectively ($P = 0.34$, Fig. 4.2) and initial heights were 199 and 225 cm, respectively ($P = 0.24$, Fig. 4.3). When stem positions within severing treatments were averaged, severing had little effect on diameter ($P = 0.32$) or height growth ($P = 0.08$) of the IS and IC treatments. Diameter growth for the severed and unsevered ramets was 4.9 and 3.2 mm while height growth was 1.6 and 1.9 cm, respectively.

Similar to the comparison between mother and adjacent stems, diameter and height growth of severed and unsevered stems in the proximal and distal positions were similar along the periphery of stands (the interaction term between severing and ramet location $P = 0.45$ for height growth and $P = 0.99$ for diameter growth, Fig. 4.2, 4.3). When the proximal and distal stems were averaged, initial diameters in PS and PC plots were similar with means of 8.9 and 8.8 mm, respectively (Fig. 4.2). However, diameters of the ramets in the PS plots grew 3.1 mm while those in the PC treatment grew 2.6 mm ($P = 0.02$). Initial heights and height growth of the PS and PC treatments were similar with 78.1 and 77.0 cm initial height (Fig. 4.3) and 7.1 and 6.6 cm height growth, respectively.

As would be expected, leaf gas exchange (A_{net} , g_s , C_i), VWC, and Ψ all varied during the growing season (Figs. 4.4 – 4.8). There were no interactions involving date so separate analyses for each date were not conducted. Stem location had no effect on leaf gas exchange for mother vs. adjacent stem or proximal vs. distal stem comparisons ($P > 0.1$, Figs. 4.4 – 4.8). The interactions between severing and ramet location were not significant for leaf gas exchange variables or soil VWC ($P \geq 0.18$).

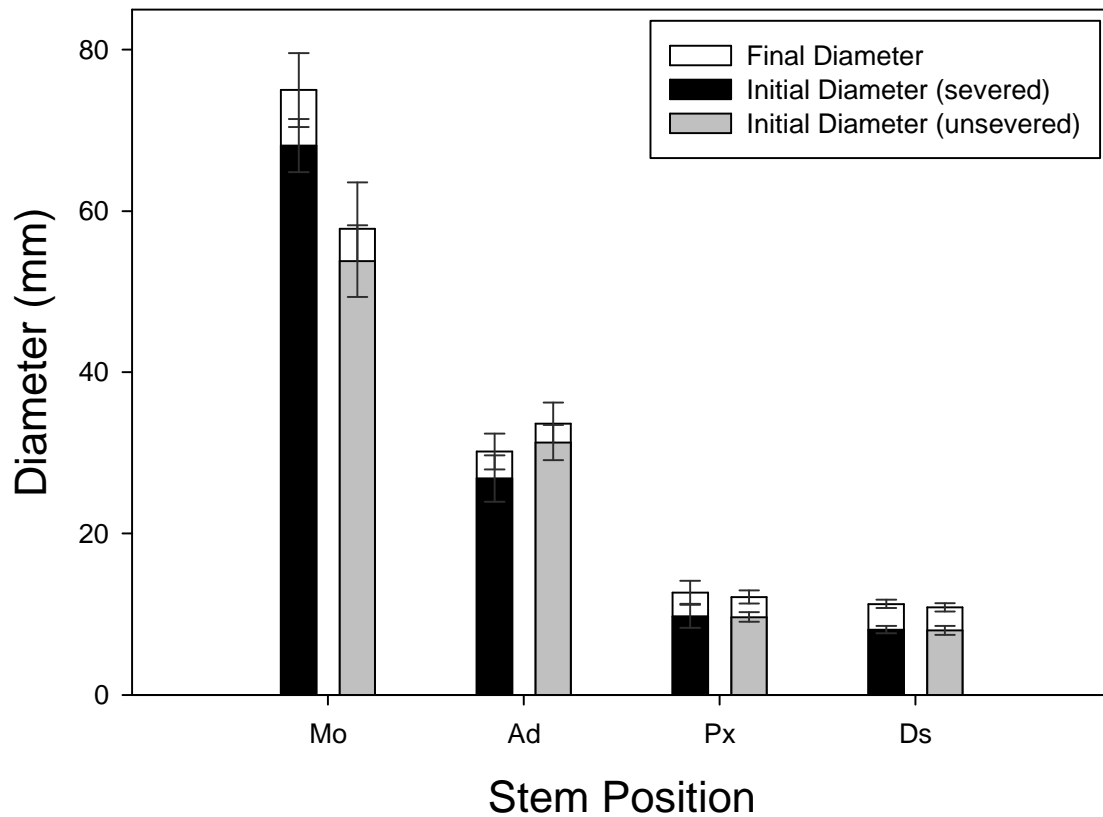


Figure 4.2. Diameter means ± 1 SE (mm) for Chickasaw plum ramets in Woods County, Oklahoma, 2008. Mo indicates mother stems; Ad, those adjacent to mothers; Px, stems on the proximal side of the peripheral severing treatment; and Ds, stems on the distal side of the peripheral severing treatment ($n = 5$).

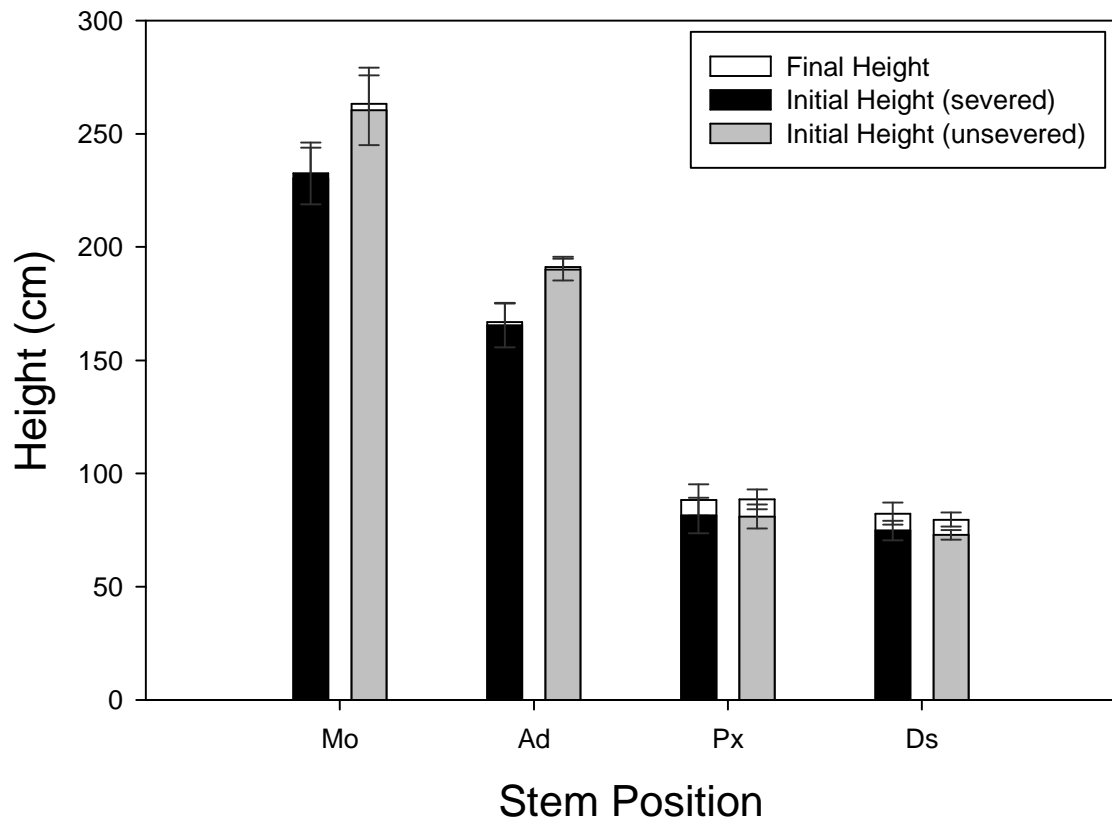


Figure 4.3. Height means ± 1 SE (cm) for Chickasaw plum ramets in Woods County, Oklahoma, 2008. Mo indicates mother stems; Ad, those adjacent to mothers; Px, stems on the proximal side of the peripheral severing treatment; and Ds, stems on the distal side of the peripheral severing treatment ($n = 5$).

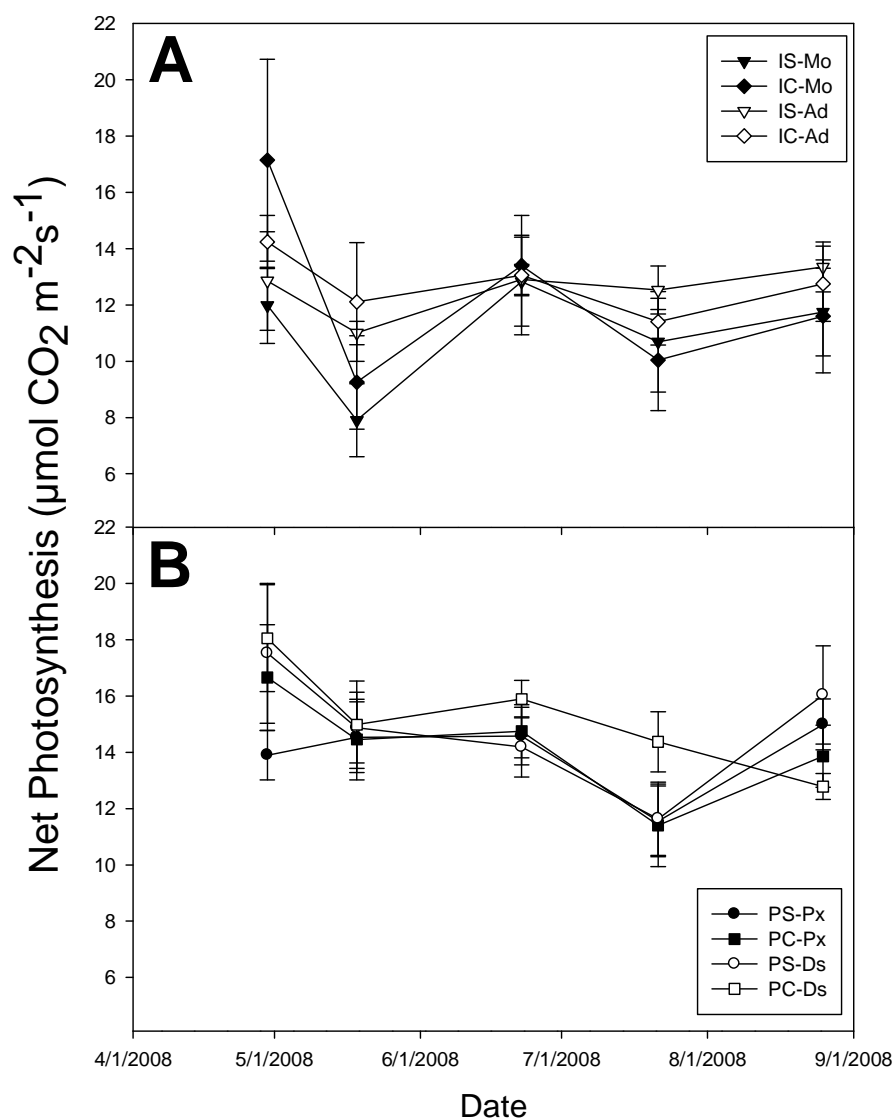


Figure 4.4. Net photosynthesis ± 1 SE ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) for Chickasaw plum ramets in Woods County, Oklahoma, 2008. **A**, internal treatments. **B**, peripheral treatments. IS indicates internal severance; IC, internal control; PS, peripheral severance; PC, peripheral control; Mo, mother stems; Ad, stems adjacent to mothers; Px, stems on the proximal side of peripheral plots; and Ds, stems on the distal side of the peripheral plots ($n = 5$).

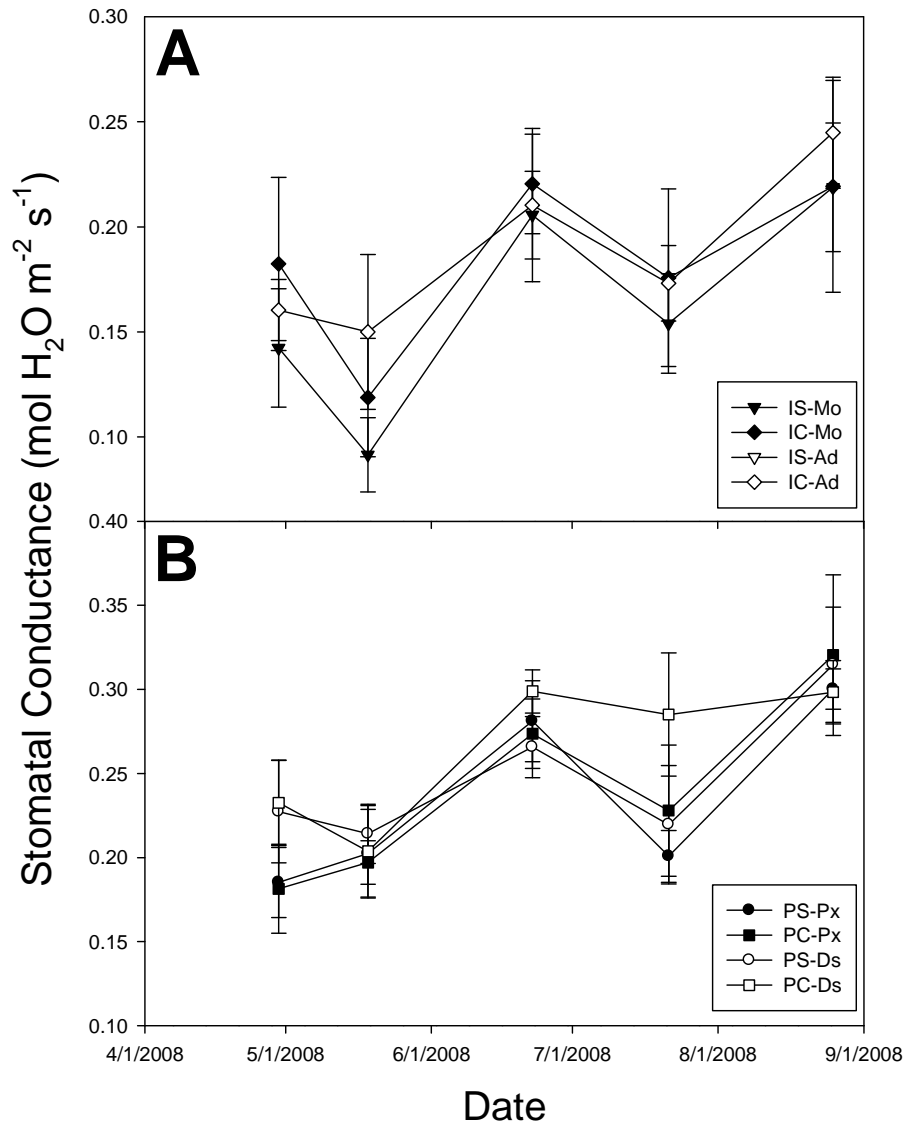


Figure 4.5. Stomatal conductance ± 1 SE ($\text{mol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) for Chickasaw plum ramets in Woods County, Oklahoma, 2008. **A**, internal treatments. **B**, peripheral treatments. IS indicates internal severance; IC, internal control; PS, peripheral severance; PC, peripheral control; Mo, mother stems; Ad, stems adjacent to mothers; Px, stems on the proximal side of peripheral plots; and Ds, stems on the distal side of the peripheral plots ($n = 5$).

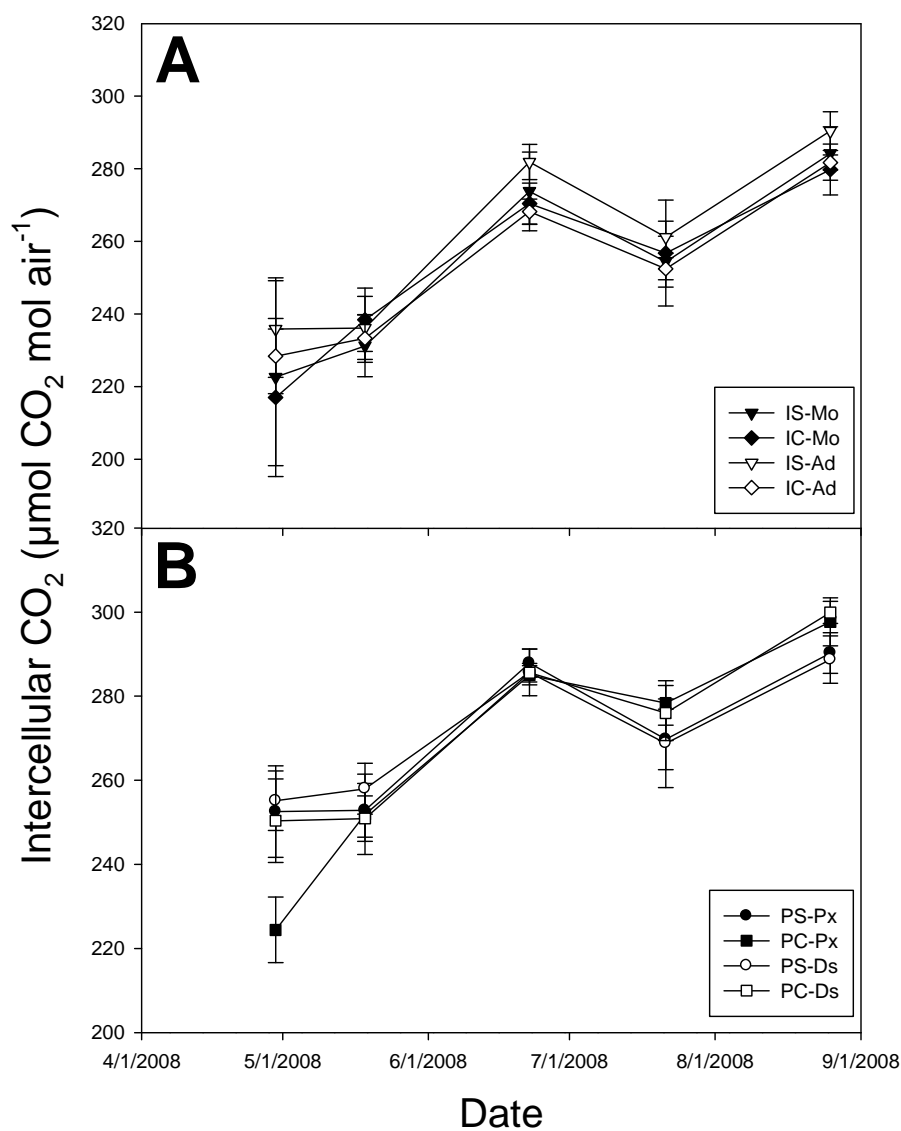


Figure 4.6. Intercellular CO₂ ± 1 SE (μmol CO₂·mol air⁻¹) for Chickasaw plum ramets in Woods County, Oklahoma, 2008. **A**, internal treatments. **B**, peripheral treatments. IS indicates internal severance; IC, internal control; PS, peripheral severance; PC, peripheral control; Mo, mother stems; Ad, stems adjacent to mothers; Px, stems on the proximal side of peripheral plots; and Ds, stems on the distal side of the peripheral plots (*n* = 5).

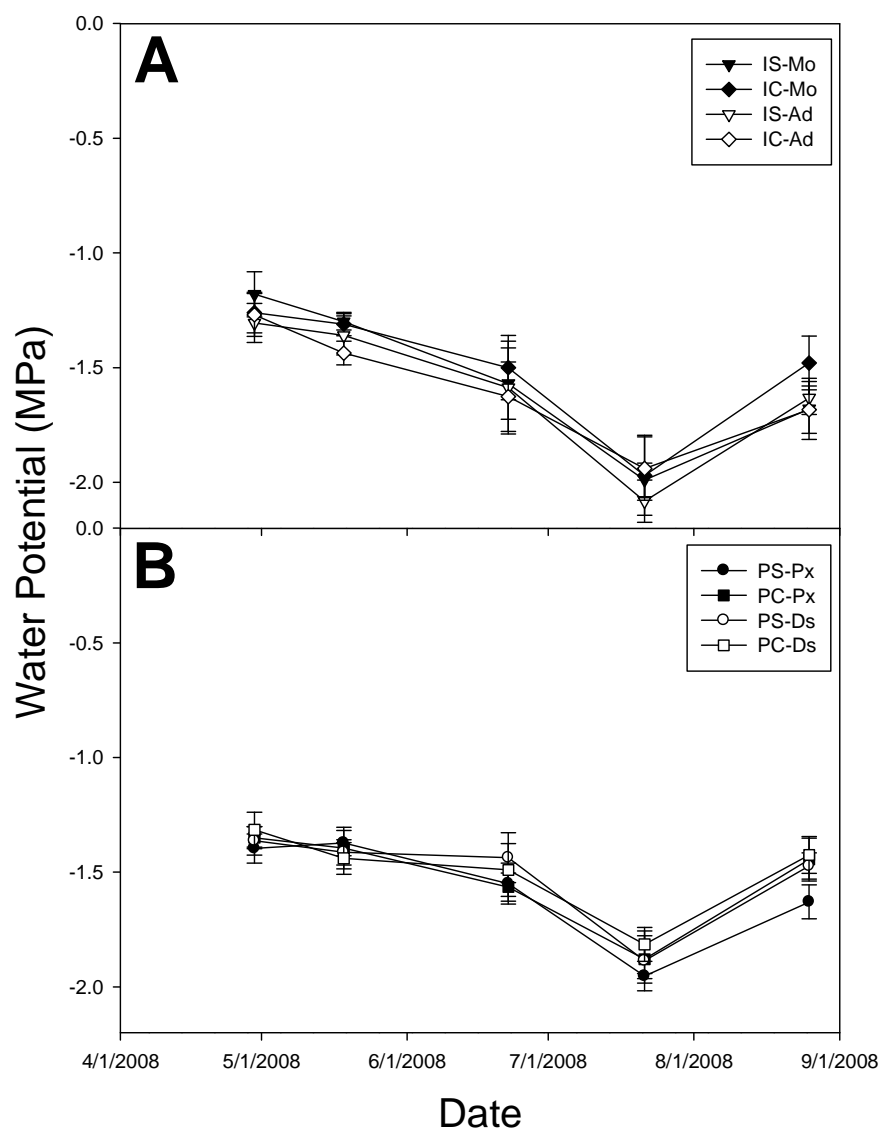


Figure 4.7. Midday stem xylem water potential ± 1 SE (MPa) for Chickasaw plum ramets in Woods County, Oklahoma, 2008. **A**, internal treatments. **B**, peripheral treatments. IS indicates internal severance; IC, internal control; PS, peripheral severance; PC, peripheral control; Mo, mother stems; Ad, stems adjacent to mothers; Px, stems on the proximal side of peripheral plots; and Ds, stems on the distal side of the peripheral plots ($n = 5$).

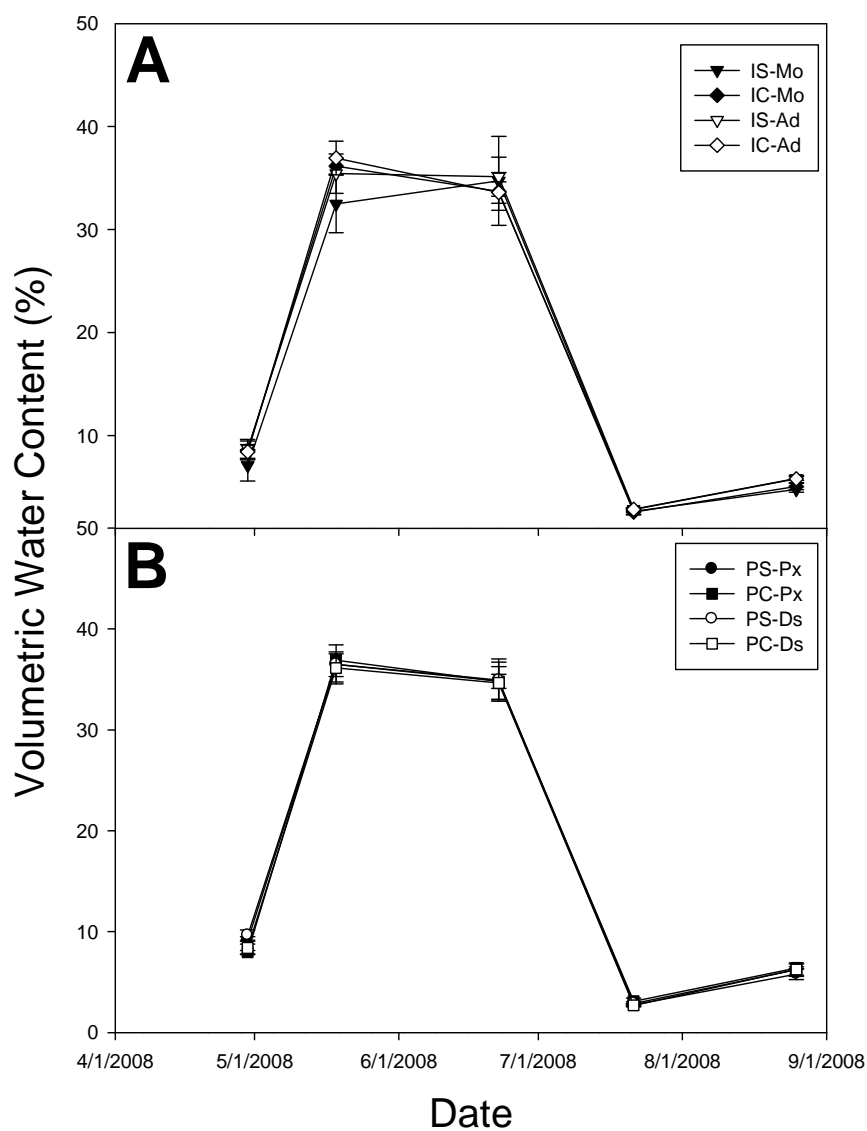


Figure 4.8. Soil volumetric water content ± 1 SE (%) for Chickasaw plum ramets in Woods County, Oklahoma, 2008. **A**, internal treatments. **B**, peripheral treatments. IS indicates internal severance; IC, internal control; PS, peripheral severance; PC, peripheral control; Mo, mother stems; Ad, stems adjacent to mothers; Px, stems on the proximal side of peripheral plots; and Ds, stems on the distal side of the peripheral plots ($n = 5$).

DISCUSSION

In general, there was little evidence of resource sharing among interconnected stems of Chickasaw plum. Severing did not affect carbon gain as measured by A_{net} or growth. Consistent with our findings, the importance of resource integration to maintain growth rates among interconnected ramets of several herbaceous species is questionable (Pauliukonis and Gough 2004; Wang et al. 2004; Poor et al. 2005; Matlaga and Sternberg 2009). Ramets of Chickasaw plum, though integrated with the clone, appear to be functionally independent when they establish root systems of their own. However, other plants species rely on resource integration to support adjacent new ramets or transfer resources from ramets in resource-rich patches to ramets in resource-poor patches (Wijesinghe and Handel 1994; Railing and McCarthy 2000; Zhang et al. 2003; Herben 2004). When resource sharing does occur, growth of ramets providing the resource subsidy may not be affected due to increases in resource use efficiency (Zhang and He 2009) which may mask the importance of resource sharing. I did not find a difference in C_i , a surrogate for the efficiency of water use, to indicate any evidence of compensation associated with sharing of water among ramets.

I did not find an effect of severing on soil moisture or leaf gas exchange in Chickasaw plum. However, I did not measure changes in ramet leaf area or root development, which influence surface areas available for water use and water uptake. In *Carex* L. the quantity of water transported from a watered ramet to an un-watered ramet was related to leaf area (deKroon et al. 1996). Additional studies might gain insight by

measuring structural differences like changes in leaf area or root density (Williams and Cooper 2005) or physiological modifications, e.g. nutrient use efficiency (Zhang and He 2009), that can modulate or eliminate adjustments in growth or gas exchange processes. Moreover, this study focused on water relations and growth as the primary factors associated with resource sharing. Nutrient amendments (Zhang et al. 2006) and stable isotopes of ^{13}C and ^{15}N (Moing and Gaudillere 1992) could be used to monitor the allocation of nutrients and fixed carbon to give a more complete description about the function of persistent connections within Chickasaw plum clones. Furthermore, resource subsidies may become apparent on sites where resource availability is particularly heterogeneous or abundant (Alpert 1999; Herben 2004; Zhang et al. 2008), in new growth following disturbance (Landhausser and Lieffers 2002), or in drought years when plants may have to rely more on stored or shared resources. Alternatively, rather than resource integration, the function of persistent connections been shown to be an effective adaptation to withstand wind erosion in dry climates in the grass *Psammochloa villosa* Trin. (Yu et al. 2008).

American plum (*P. Americana* Marsh.) in Kansas tallgrass prairie accessed water from the upper 25 cm of the soil profile (McCarron and Knapp 2001). I conducted exploratory excavations and found the majority of the lateral and fine roots of Chickasaw plum also were within the upper 25 cm of the soil profile. However, I also found that tap roots under a stem can extend beyond 2 m and that occasional deep sinker roots occur along lateral connections between ramets. This architecture suggests that Chickasaw plum can access water from the top of the soil profile in the spring and after summer

precipitation events as well as water from deeper in the soil profile. These sinker roots may decrease the need for water sharing among ramets of Chickasaw plum.

Stem sizes were different according to their location with largest clones in the center of a stand and progressively smaller ramets with distance from the mother. This is consistent with the description of Chickasaw plum clones by Dunkin et al. (2008). The peripheral ramets (Px and Ds) in the PS plots experienced more diameter growth than the comparable stems in the PC plots. This result is somewhat counter-intuitive because if severing were to alter growth, it would be expected to increase growth of one location at the expense of the other location (Wijesinghe and Handel 1994; Zhang and He 2009).

Chickasaw plum clones, though interconnected, appear to have ramets that are functioning independently of each other relative to water relations, leaf gas exchange, and growth. For those trying to restore native prairie or provide a woody element in grassland habitats, this research emphasizes that Chickasaw plum is well adapted to semi-arid, sandy conditions and a disturbance which severs the roots of a plum stand will not harm the remaining stems. Therefore, management to hasten the expansion of Chickasaw plum clones by severing and transplanting ramets in areas without shrubs has the benefit of increasing woody cover without risking negative effects on the remaining ramets. These adaptations allow Chickasaw plum to thrive in a wide range of site conditions and probably contribute to the moderate success of severed transplants used for propagation.

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Candidate for the Degree of Master of Science

Major Field: Natural Resources Ecology and Management

Scope and Method of Study: I tested the effects of tillage, planting date, and competition control on the survival and growth of different propagule types (bare-root seedlings, coppiced transplants, and intact transplants) of Chickasaw plum (*Prunus angustifolia*), smooth sumac (*Rhus glabra*), and fragrant sumac (*R. aromatica*). In another experiment, I severed the roots between interconnected ramets on the interior and periphery of Chickasaw plum stands and left undisturbed control plots for comparison. Growth (diameter and height), net photosynthesis, stomatal conductance, intercellular CO₂ concentration, midday stem water potential, and soil volumetric water content of interconnected ramets were monitored to determine if ramets on one side of the severance were receiving carbon or water resource subsidy from ramets on the other side.

Findings and Conclusions: In the first experiment, tillage did not affect survival or growth. After 2 years, plum seedlings had >50% higher survival than coppiced and intact transplants. Planting in late spring increased survival of plum coppiced transplants by >33%. Competition control with weed barrier cloth increased plum survival by 13% and diameter growth by 0.5 mm in the first year. For smooth sumac, there were no differences in survival and growth between CT and IT and survival was 49% after 2 years. For fragrant sumac, 83% of bare-root seedlings survived after 2 years. Overall, seedlings performed well, but if seedlings are not available, local transplants can be taken and planted at higher densities to achieve similar results. In the second experiment, severing had little or no effect on growth, photosynthesis, stomatal conductance, intercellular CO₂, stem water potential, and soil water. Though Chickasaw plum possesses persistent root connections between ramets there is minimal evidence of water or carbon resource integration between interconnected ramets under normal conditions.

ADVISER'S APPROVAL: Rodney E. Will
